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NEARSHORE BENTHOS OF LAKE ONTARIO 1981 AND 1991

VOLUME I - MAIN FINDINGS

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NEARSHORE BENTHOS OF LAKE ONTARIO

1981 AND 1991

VOLUME I - MAIN FINDINGS

Report prepared by:

Water Systems Analysts

Report prepared for:

Ontario Ministry of Environment and Energy
Environmental Monitoring and Reporting Branch
Surface Water Section

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REFERENCE NOTE

The activities described in this report were partially carried out when the Ministry was the Ministry of Environment (MOE). In February 1993, MOE was merged with the Ministry of Energy to form its current name of Ministry of Environment and Energy (MOEE). Notations in this report of Ministry of Environment refer to activities prior to February 1993. When MOEE is used, it refers to events or activities after February 1993.

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LIST OF ABBREVIATIONS

ANOVA	analysis of variance
BACI	before-after control-impact study design
CA	correspondence analysis
cm	centimetre
mm	millimetre
m	metre
MDS	multiple dimensional scaling ordination
QA/QC	quality assurance/quality control
Shannon H′	Shannon diversity index
TWINSPAN	two-way indicator species analysis
um	micron

EXECUTIVE SUMMARY

During August and September of 1991, a resurvey of the nearshore zone (5 and 20 m) benthos of the Canadian side of Lake Ontario was conducted. The main objective of this study was:

(1) to repeat a 1981 survey of the nearshore zone of Lake Ontario to determine if changes in benthic invertebrate communities suggest improvement in water quality over the 10-year period.

Secondary objectives were to:

(2) re-evaluate the influences of the modifying factors identified during the 1981 survey (i.e., substrate, exposure, upwelling) to determine if associations between invertebrates and these factors are consistent when there are changes in water quality;

(3) determine if changes in benthic community structure over the 10-year period were related to the presence of zebra mussels;

(4) examine the associations of sphaeriids and zebra mussels to determine if there was any evidence of an effect (positive or negative) on sphaeriid clams and unionids; and

(5) document variations in size class structure during the initial periods of colonization to confirm the timing of first settlement.

Differences in the composition of benthic invertebrates were observed between 1981 and 1991 that suggested that changes in water quality had occurred. Changes were more obvious from the 5-m communities than they were from the 20-m communities. At 5 m,

changes suggestive of improvements in water quality were generally widespread and demonstrated by increases in taxonomic richness, and increased numbers of insects (Ephemeroptera, Chironomidae) and gastropods. At 20 m, communities along the north shore of the lake exhibited changes that also suggested improvements in water quality with increases in numbers of lumbriculids, gastropods and sphaeriids. Along the Niagara-Hamilton corridor, reductions in the numbers of chironomids at 20 m was a surprising observation suggesting the effect of factor unrelated to the expected enrichment scenario. Because of subtle differences in the methods and timing of surveys between 1981 and 1991 the interpretation of the results are, however, subject to a degree of uncertainty.

Of those habitat descriptors that we studied, depth had the most obvious effects on community structure. In general, 5-m communities were characterized by epibenthic fauna such as gastropods and insects (chironomids, Ephemeroptera, Trichoptera). In contrast, 20-m communities were characterized by infaunal groups such as sphaeriid clams and oligochaete worms. During 1981, the 5-m community was more similar to the 20-m community because of a higher proportion of worms and was attributed to the more nutrient-enriched conditions at that time. In 1991, after improvements in water quality, gastropods and insects were more dominant.

Other habitat descriptors had only weak effects on community structure and/or the observed associations were more easily explained by spatial patterns thought to be related to spatial variation in water quality. The effects of upwelling in Lake Ontario postulated by Barton (1986; J. Gt. Lakes Res. 12:270-280) were not evident in the 1991 survey, mainly because insects such as Ephemeroptera were more prevalent along the north shore of the lake. Barton felt that upwelling cold waters on the north shore was the cause of a reduced community of insects, particularly Ephemeroptera. In contrast to the other Great Lakes, Lake Ontario still has a depauperate insect community in the nearshore zone. This suggests that in relation to the other lakes, upwelling in Lake Ontario does structure the benthic community.

The presence of zebra mussels at 5 m between Niagara and Hamilton did not cause changes in community composition at major taxonomic levels. However, there was some suggestion that zebra mussels caused changes in species-level composition. The primary effect appeared to be a change in the composition of the gastropod communities. In communities with zebra mussels, Valvata tricarinata and Pleurocera acuta were dominant hmembers of the gastropod community, whereas in communities without zebra mussels, Probythinella lacustris was more dominant. There were no obvious effects of zebra mussels on composition of the bivalve community.

Density of zebra mussels in the western end of Lake Ontario during 1991 varied between 611 m^{-2} at Bronte, to over 24,000 m^{-2} at Niagara-on-the-Lake and was lower than peak numbers found in the other Great Lakes (up to 400,000 m^{-2}). Based on size class structure, zebra mussels entered and settled along the shoreline between Stoney Creek and Oakville in the fall of 1990, and between Niagara-on-the-Lake and Beamsville during the spring of 1991.

Quagga mussels (Dreissena sp.) were found between Niagara-on-the-Lake and Beamsville, and at Oakville. The presence of large mussels at Beamvsville suggested that settlement occurred sometime in 1990.

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1.0 INTRODUCTION

In 1981, as part of a study conducted by the Ontario Ministry of the Environment, benthic macroinvertebrates were collected from the nearshore zone of Lake Ontario (Integrated Explorations, 1984) to describe the distribution of benthic invertebrates in relation to physical characteristics and examine associations among the benthic taxa (Integrated Explorations, 1984; Barton, 1986). The purpose of that study was to make biologically-based inferences on environmental conditions and to examine relationships between natural environmental factors and the composition of benthic invertebrate communities in the nearshore zone of the lake. Benthic communities described during that survey suggested that areas near the mouth of the Niagara and Humber Rivers, and areas at the far eastern part of the Lake (near Prince Edward Point) were eutrophic. In the central and northeastern parts of the lake (eastern Scarborough to Ostrander Point) the effects of exposure and upwelling resulted in low standing stocks of chironomids and other insects.

Numerous studies of benthic invertebrates in the Great Lakes have been conducted because of the wide-spread and long-standing use of benthic invertebrates as indicators of environmental conditions. However, few studies have been geographically broad in nature. In 1972 and 1973, Barton (1988) surveyed the nearshore zone of Lake Erie and described the depth and substrate preferences of the 20 most dominant taxa. In 1978 and 1979, Krieger (1984, 1985) sampled the nearshore zone of the central basin of Lake Erie and described the communities associated with degraded conditions. In 1980, Barton and Griffiths (1984) sampled the nearshore zones of eastern Lake Huron, Georgian Bay and North Channel and found that benthic community structure was related to exposure to wave action, local geology, depth, and substrate. Between 1978 and 1980, Winnel and Jude (1984) illustrated the associations between Chironomidae and sand substrates in the nearshore zone of Lake Michigan.

Most of the historical work on the nearshore benthic organisms of the Great Lakes was conducted during periods when the Great Lakes were more nutrient enriched and, therefore, reflect those conditions. In the past 10 years there have been improvements in a variety of aspects of the water quality of the Great Lakes (e.g., De Vault et al., 1994; Neilson et al., 1994; Minns et al., 1986). There is potential for these changes in water quality to result in changes in nearshore benthic community structure, but little work has been conducted to determine if this is true (Nalepa, 1991). In addition, the recent introduction of the zebra mussel (Dreissena polymorpha) to the Great Lakes (Hebert et al., 1989; Griffiths et al., 1991) has the potential to significantly alter the ecology of benthic invertebrate communities, particularly in the nearshore zones where substrate and temperatures are suitable for zebra mussels. At the time this work was conducted, zebra mussels were distributed throughout the whole of Lake Erie and only partially through Lake Ontario (Griffiths et al., 1991). Consequently, a re-survey of the nearshore zone (where colonization potential of the zebra mussel is greatest) was timely.

The main objective of this study was to repeat the 1981 survey of the nearshore zone of Lake Ontario to **(1) determine if changes in benthic invertebrate communities suggest improvement in water quality over the 10-year period.** A secondary objective was to **(2) re-evaluate the influences of the modifying factors identified during the 1981 survey (i.e., substrate, exposure, upwelling; Barton, 1986) to determine if associations between invertebrates and these factors are consistent when there are changes in water quality.** In this study, the associations between invertebrate community structure and likelihood of upwelling, exposure, % cover of Cladophora, depth, substrate classification, and location were examined. A third objective was to **(3) determine if changes in benthic community structure over the 10-year period were related to the presence of zebra mussels.** Some investigators have suggested that zebra mussels negatively affect native bivalves, particularly unionids (e.g., Mackie, 1991, 1993). However, there are few data on the effects of zebra mussels on other native bivalves such as the Sphaeriidae. In Lake Ontario, the numbers of unionids are lower than in the other Great Lakes, whereas, the numbers of sphaeriid clams are more similar to the other lakes. A survey of the nearshore zone allows for examination of the associations between sphaeriid clams, unionids and zebra mussels. Consequently, a fourth objective of this study was to **(4) examine the associations of sphaeriids and zebra mussels to determine if there is any evidence of an effect (positive or negative) on sphaeriid clams and unionids.** Finally, this collection of zebra mussels provided an opportunity to **(5) document variations in size class structure during the initial periods of colonization.** Information on size class distributions in this instance might be useful for establishing the timing of first settlement.

In 1981, the survey by Integrated Explorations included sampling at multiple times of the year (monthly from July to mid November), and at multiple depths (2, 5, 10, 20 m) and on various substrate classifications. The most complete survey of the lake was conducted in July at each of the depths. An examination of the historical data suggested that there was a broader variety of substrate classes at the 5 and 20 m depths, and that most of the spatial and depth-related variation in invertebrate assemblages could be represented by results from the 5 and 20 m samples alone. Therefore, in 1991 sampling was conducted at these depths only. The original stations were revisited once during late-summer of 1991. Because of logistical constraints, samples were collected up to one month later in 1991 than in 1981. The seasonal data in 1981, in addition to other studies have been used to evaluate the possible effect of seasonality on the 1981-1991 comparison.

The focus and approach of this study is different from the typical pollution-related investigations using benthic invertebrates. The majority of stations were located in areas away from major point-sources of pollutants and outside of locations known to be heavily impacted by anthropogenic activity. The stations, on the whole, represent background conditions along the nearshore of Lake Ontario's Canadian shoreline.

2.0 METHODOLOGY

Generally, the sampling methods described by Integrated Explorations (1984) and Barton (1986) for the 1981 survey were used during this study. The survey was conducted between August 7 and September 5, 1991. Two kinds of benthic samples were collected: (1) meio-scale samples for an assessment of the general benthic community; and (2) macro-scale samples for an assessment of the association among bivalve taxa. Meio-scale samples were collected using either airlift suction samplers (Integrated Explorations, 1984) or sediment corers. Macro-scale samples were collected by scraping zebra mussels, associated debris, and other obvious bivalves from within 1 m^2 quadrats. Collection methods are described by Integrated Explorations (1992), however, brief descriptions of the methods are outlined in the following sections.

2.1 Meio-Scale Benthos Communities

2.1.1 Sample Collection

Meio-scale samples were collected at each of two depths (5 and 20 m) from each of 25 Transects (Figure 1) by divers equipped with SCUBA. These sampling locations were as close as achievable given positioning techniques to the locations used in the 1981 survey by Integrated Explorations (1984). The 1981 locations were determined using Loran C and compass sightings to shore reference points. Photographs of shore reference points were also taken for all stations in 1981. In 1991, station positions were located using Loran C, navigation charts and the 1981 reference photographs. At each depth and transect combination (2 depths x 25 transects = 50 stations) there were three replicate samples collected (total number of samples = 150). Samples were collected using either an airlift sampler for rock or other hard substrate, or a corer for soft substrate. Both devices had a 10 cm inner diameter. When used, corers were penetrated to a depth of ≈ 12 cm into the substrate. Debris collected by the airlift samplers were captured in bags made of 200 μm Nytex™ mesh. The sampled area was generally 78.5 cm^2, but ranged to 929 cm^2 at stations where the amount of debris was judged to be minimal (Integrated Explorations, 1992). Debris from both corers and airlift samples were preserved on site with 10% buffered formalin to prevent spoilage.

2.1.2 Sample Processing

All benthos samples were stained with Biebrich-Scarlet dye to improve visibility of preserved organisms and washed using 200 µm mesh to remove excess preservative, dye, and debris. Samples were scanned under a binocular microscope at 6-12x magnification to further improve visibility of benthic invertebrates. Benthos were removed from the debris and re-preserved in 70% ethanol until they were identified. Sorting efficiencies were ≥ 90% (recovered 90% of the organisms) for all samples (Appendix A). Nematodes were not kept because they were considered too small to be retained with any efficiency with 200 µm mesh, and because they were not kept by Barton (1986). Aquatic Acarina were apparently not kept when the 1981 samples were sorted (see data matrix in Integrated Exploration, 1984) but were kept when the 1991 samples were sorted.

Many of the samples were "split" to reduce the time needed for sorting. In most cases, sorting required 3-4 hours. Splitting, or sub-sampling, was performed by spreading samples thinly over a white enamel tray, and separating the debris into equal parts by eye. For all samples, the minimum amount of material examined was 25%. The sub-sampling technique did not treat taxa differentially (Appendix B) and likely did not influence patterns in community structure identified in the detailed analyses which are described below.

2.1.3 Identification

Benthic invertebrates were identified following the standards described by the Ontario Ministry of Natural Resources (OMNR, 1985). Chironomids from each sample were sorted into like groups and a minimum of 10% of the organisms within each group were slide mounted in polyvinyl lactophenol to make important features of the head capsules easier to see. In many samples, chironomids were dominated by small individuals. In these cases, it was difficult to distinguish taxa based on external features, so all individuals were slide mounted. Oligochaetes were sub-sampled to provide a minimum of 50 and maximum of 100 individual specimens and were warmed for 24 hours in lactophenol to clear the bodies. They were temporarily mounted on 5x15 cm slides and covered with oversized cover slips. Phase-contrast microscopes were used to distinguish general morphology and to discern the shape of the setae and penis sheaths.

The taxonomic keys used for identification of the various taxa found in the survey are listed in Table 1 along with the personnel that made the identifications. External opinions were obtained for all oligochaete and chironomid taxa, and for selected (difficult) taxa from the other major groups (Table 1). Reference collections have been retained by the Ontario Ministry of the Environment & Energy (E.T. Howell), and by Water Systems Analysts (B.W. Kilgour).

For the purposes of the meio-scale sample analysis, all dreissenid bivalves were considered zebra mussels (D. polymorpha). Specimens from the meio-scale survey were identified prior to the general acceptance of a second form of dreissenid, the "quagga" mussel (Dreissena sp.) (May and Marsden, 1992). During processing of macro-scale samples, some dreissenids (1%) were identified as quagga mussels. Given the low percentage of quagga mussels in the samples, it was not considered necessary to re-identify the dreissenids from the meio-scale survey.

All of the raw density data for each taxon collected in 1991 are available in Appendix C.

2.1.4 Benthic Community Indices

Summary benthic indices calculated with the data included:

- Shannon's H' (Shannon and Weaver, 1949)

$$H' = \sum p_i \log_2 p_i \qquad [1]$$

where, p_i refers to the proportion of the total numbers accounted for by the ith taxon.

- Richness (number of taxa per sample and per station)

Shannon's H' values are based on information theory and indicate the uncertainty of encountering a taxon in a sample. Generally, higher values indicate the presence of more taxa in a sample (Washington, 1984). Historically, higher Shannon values have been associated with better water quality. However, Shannon H' values tend to be more discriminating when differences in water quality are obvious and less so when differences in water quality are more subtle (Metcalfe, 1989).

Abundance of 18 major taxonomic groups (Enchytraeidae, Lumbriculidae, Naididae, Nemertea, Polychaeta, Tubificidae, Isopoda, Amphipoda, Ephemeroptera, Trichoptera, Tanypodinae, Diamesinae, Orthocladiinae, Chironomini, Tanytarsini, Gastropoda, Unionidae, and Sphaeriidae) were calculated to simplify analyses and interpretation. Some (e.g., Furse et al., 1984; Warwick, 1988) recommend the use of family-level taxonomy because effects of disturbance are often manifested at family-level characteristics. Richness (= number of distinct taxa in a sample) was also calculated for each sample. Number of taxa should increase when the environmental tolerances of more taxa are met.

2.1.5 Station Descriptions

At each station (transect and depth combination), notes on the substrate composition within a 2-5 m radius of sampling areas, were made and included substrate class, coverage by Cladophora and zebra mussels (if present), and surface and bottom temperatures (Integrated Explorations, 1992). Substrate at each site was also coded based on the predominant type of material present (Integrated Explorations, 1992): 1 for bedrock, boulder and cobble; 2 for gravel; 3 for sand; 4 for silt; and, 5 for clay. These values were used in later analyses of correlations between benthic community structure and substrate type. Liability to sudden temperature changes (due to internal sieches in the lake) should be related to distance to the main basin of the lake, the slope of the nearshore zone, and position relative to the prevailing wind (Barton, 1986). This was approximated as the distance from each station to the 50 m contour which is the shallowest uninterrupted contour encompassing the main basin of Lake Ontario (Barton, 1986). Exposure can be thought of as the likelihood of experiencing heavy wave action. This should be related to fetch, or the unobstructed distance from the station to an opposite shore. To describe exposure, the unobstructed distance from each station to the nearest shore in each of eight compass directions (N, NE, E, SE, S, SW, W, NW) was determined from Canadian Hydrographic Service maps which were generally at scales of ≈ 1:70,000.

2.2 Macro-Scale Bivalve Communities

One of the objectives identified in the introduction was to determine if zebra mussels were responsible for changes in numbers of sphaeriids and unionids. The meio-faunal samples were not expected to do a good job of collecting unionids if they were present. Consequently, to augment the meiofauna data, additional (five) bottom samples were collected at 5 m at Transects 1-5 and 7-9 (Figure 1). Samples were collected by placing a 1 m^2 quadrat on the bottom and collecting zebra mussels and other bivalves from an area of either 0.25 or 1 m^2 (depending on the number of mussels). Debris from within the quadrat was collected using either an airlift sampler when the debris was fine, or by lifting rocks in a bucket to the surface when the bottom was irregular and coarse (Integrated Explorations, 1992). All mussels and associated debris were preserved in 10% buffered formalin. In the laboratory, mussels and other bivalves (unionids, sphaeriids) were removed from the substrate and re-preserved in either buffered formalin (zebra mussels) or in 70% ethanol (unionids, sphaeriids). All bivalves from each sample were counted and identified to species. Shell length of up to 200 zebra mussels from each sample, and all quagga mussels were recorded.

2.3 Data Analysis

2.3.1 Matching 1981 and 1991 Meio-Benthic Data Bases

Prior to any statistical evaluations using the 1981 and 1991 data sets, some taxonomic differences had to be clarified. Since 1981, some taxonomic revisions have been made. Consequently, taxa which were identified as one species in 1981 were given new names to be consistent with 1991 taxa. Also, some individual taxa recorded in 1981 could have been one of multiple taxa in 1991. In these cases, the original names were used because it was difficult to make any confident changes in taxonomy. The specific changes to the 1981 taxonomy are given in Table 2. These changes in taxonomy may not have been necessary because the data analyses were conducted largely with summary variables (family-level or higher). However, the changes are described so that future studies, which might require more precise taxonomy, can more easily understand the differences between 1981 and 1991 taxa lists. Both the 1981 and 1991 raw data sets are provided in Appendix C. For those taxa which we suggest have had name changes over the ten-year period, the raw 1981 data have the new names. Integrated Explorations (1984) provide the original raw data for the 1981 survey for those interested.

2.3.2 Analysis of Meio-Benthic Data

Of the four objectives identified in the Introduction, three were specific to the meio-benthic community ([1] determine if changes in the community reflect changes in water quality; [2] determine if the relationships between benthic communities and modifying factors have changed; [3] determine if changes in the benthic community are related to the new presence of zebra mussels). To address these objectives, we separated the statistical analyses into five specific tasks:

(1) determine whether the underlying structure of the community data could be adequately described using major-group taxonomy;

(2) determine if there was an optimal statistical transformation for abundance data to facilitate analyses;

(3) determine the power of the survey for detecting temporal changes in major taxon abundances;

(4) describe the degree and nature of variation of communty structure between years, depths and transects; and,

(5) determine the degree and nature of association between the benthic communities, habitat

descriptors and the presence of zebra mussels.

The first two tasks were preliminary to the major tasks (4 and 5) which were of primary importance. Task (3) was addressed because an understanding of the power and sensitivity of a design are needed to fully interpret the degree of changes observed (McBride et al., 1993; Reckhow, 1994). How each of these questions was addressed is described in detail below.

2.3.2.1 Assessing Taxonomic Levels

Much of the preliminary work in this project involved identification of taxa to species. In the combined 1981-1991 data set there were 169 taxa. Although it is possible to statistically analyze differences between communities with data sets that include as many taxa, it is somewhat difficult to interpret the causes of observed differences. It is very common for studies describing variations in benthic community structure to use higher levels of taxonomy (Family, Order). In fact, some investigators feel that higher-level taxonomy provides as much resolution for assessment of environmental quality as does lower-level (Species) identification (Furse et al., 1984, Warwick 1988a,b; Ferraro and Cole, 1990, 1992, Warwick et al., 1990). In terms of making our statistical analyses more biologically interpretable, it was desireable to justify an analysis based on higher taxonomic levels. This was done by comparing a distance matrix (Bray-Curtis) based on the complete species list with a distance matrix (Bray-Curtis) based on the 18 summary taxa. If the distance matrix based on the higher-level taxonomy was highly and significantly correlated with the distance matrix based on the lower-level (Species) taxonomy, then the relationships between samples (Stations, Transects, Depths, etc.) would be maintained whether we analyze a data set based on species or based on higher levels. Mantel's test (Mantel, 1967; Legendre and Fortin, 1989) was used to test for such an association between the two distance matrices using NTSYSpc software (Rohlf, 1993). In this case, Mantel's test showed that there was a highly significant correlation between the two distance matrices (Mantel's $r=0.77$; $p<0.001$) suggesting that the use of the 18 summary taxa would provide information which was similar to that we would have obtained if the complete data set had been analyzed. We therefore used major-group taxonomy for the majority of the following analyses.

2.3.2.2 Assessing Transformations

Prior to any statistical analyses, Taylor's Power Law (Taylor, 1961) was used to determine if there was an optimal transformation that could be applied to normalize the major-taxon densities. Taylor's Power Law examines the relationships between station means and variances. The slope of the relationship between log s^2 (variance) and log X (density) is b, the index of aggregation. The exact variance stabilizing function can be calculated once the index of aggregation is known (Taylor, 1961): $X' = X^{1-(b/2)}$, where X' is the transformed datum. In this analysis, slopes for the 18 major taxa were between 0.5 and 0.7. This suggested optimal transformations of between $X^{0.65}$ and $X^{0.75}$. Results of the statistical analyses carried out on either raw data, or data transformed using ln(x+1) or the recommended transformations were not different. Therefore, the analyses described below are for untransformed data to improve clarity.

2.3.2.3 Assessing Power of the Survey for Detecting Temporal (Year) Differences

The first objective of this study was to determine the degree of change in community structure between 1981 and 1991. The first step in our analysis of changes over this period was an Analysis of Variance (ANOVA) testing for changes in the summary measures and the abundances of major groups. Given the patterns in the historical 1981 data (Barton, 1986), significant variations due to depth and station location (Transect) were expected. Consequently, these factors, and their associated interaction terms, were included in the ANOVA models to control extraneous sources of variation. The specific model used for these tests is given in Table 3. Transect was considered a random variable. Variations in richness, Shannon's H', and total and individual densities of 18 major taxa were examined in this way.

Following the ANOVAs, power analysis (Green, 1989; Peterman, 1990) was conducted to determine the number of transects that would be needed to detect changes in the mean density of major taxa of varying magnitudes among sampling dates (i.e., how many transects would be needed to detect a change in the number of tubificids in Lake Ontario from one sampling period to the another?). Modifications of the equations described in Zar (1984) were used to calculate the magnitude of differences that would be detected as significant. Using Zar's figure B.1a, with degrees of freedom for date (v_1=1) and Transect (v_2=24) effects (for testing DATE with DATE·TRANSECT as error), and with Type I (α) and Type II (β) error probabilities set to 0.05, the non-centrality parameter Φ was 2.7. Since there were two groups in this study (1981, 1991) and 25 transects, the number of groups k' = 2 and the number of replications per group (Transects) n' was 25. The detectable difference (δ) was therefore,

$$\delta = \sqrt{\frac{2 \cdot K' \cdot S^2 \cdot \theta^2}{n'}} = \sqrt{\frac{2 \cdot 2 \cdot S^2 \cdot 2.7^2}{25}} = 1.08S$$

where s = the square root of the mean squared error for the YEAR·TRANSECT term. Detailed results of the power analysis are presented in Appendix D.

2.3.2.4 Describing Variation in Community Structure

In addition to the summary measures and the abundances of the 18 major groups, we also summarized community structure using a variety of multivariate techniques. Multivariate techniques often elucidate patterns in data when univariate methods fail (Clarke and Green, 1988). Specifically, we used Correspondence Analysis (Hill, 1973; Rohlf, 1993) and TWINSPAN (**T**wo-**W**ay **In**dicator **Sp**ecies **An**alysis; Hill, 1979). Correspondence Analysis (CA) was selected to ordinate the raw densities (averaged within depth-transect combinations) of the 18 major taxa because it is recognized as being somewhat robust for finding interpretable structure with macrobenthic data (e.g., Culp and Davies, 1980; Jackson, 1993). Three axes from the CA were retained and taxa were considered important to the structure of the CA axes if they contributed more than 10% to the structure of the axis and had squared correlations with the axes of > 0.30. These criteria were determined by trial and error with the objective of having sensible interpretations of the axes.

TWINSPAN was used as an alternative method for describing the multivariate data structure and is a method of dichotomized ordination analysis (Hill, 1979). In this analysis, TWINSPAN was used to order taxa (18 summary taxonomic groups) and sites based on ranked relative abundances of the taxonomic groups. The abundance rankings of taxa in samples was based on percent contribution of sample totals and were as follows: 0, not present; 1, 0-2%; 2, >2-5%; 3, >5-15%; 4, >15-25%; 5, >25-50%; 6, >50-100%. Sample groupings identified in the analysis were used to explore the affinities of taxa for years and depths. With TWINSPAN, the sample groupings are derived from the ordering of a hierarchical sample classification resulting from successive division of modified correspondence analysis axes based on taxa. The fidelity of taxa to sample groupings is used to define a classification of taxa which was also ordered, and then, incorporated with the sample ordering into a table. The final number of sample groupings is arbitrary and is a function of the minimum group size for division and the maximum levels of division specified in the analysis, as well as the intrinsic patterns of association in the data.

2.3.2.5 Assessing The Causes of Variation in Community Structure

After describing variation in community structure using CA and TWINSPAN, the next step in the analysis was to determine the causes of that variation. Specifically, we were interested in describing the relationships between the benthic community and the habitat descriptors (depth, location, substrate, fetch, upwelling) and determining if those relationships changed between 1981 and 1991. We were also interested in determining if changes occurred between 1981 and 1991 and whether any observed changes could be attributed to the presence of zebra mussels. To accomplish this complex of tasks, we used a battery of statistical testing and graphical procedures. Depending on the question, we used combinations of (1) ANOVAs on summary measures, (2) Mantel's tests, (3) statistical analyses and graphical presentation of axis scores from Correspondence Analysis, (4) examination of TWINSPAN maps and ordered tables, and (5) examination of histograms of major taxon densities. Patterns that were consistent and "picked up" by Mantel's tests, CA, TWINSPAN and taxon histograms were described in Section 3.0 and interpreted in Section 4.0.

Describing Temporal Changes

The ANOVAs on major taxon densities and summary measures described earlier was the first step in determining the nature and magnitude of changes in community structure in the lake. That initial analysis suggested that changes in community structure existed, but that it was difficult to make whole-lake statements regarding the nature of the changes due to the highly significant year·transect·depth interactions (Table 4).

To more succinctly describe changes in community structure, we tested for differences in CA axis scores between 1981 and 1991 within each of 5 and 20 m depths. Station CA scores were also plotted two axes at a time to illustrate differences. Bivariate ellipses about year-depth combinations were also plotted to show the 95% confidence regions about the year-depth centroids (multivariate means). When ellipses do not overlap, they suggest significant differences between groups. For example, to determine if there was a change at 5 m, we would compare the confidence ellipse about the 1981 5-m data with the ellipse about the 1991 5-m data. Confidence ellipses were plotted using built-in programs in SYSTAT software (Wilkinson, 1990). TWINSPAN groupings were used to confirm observed differences between years at each depth.

Associations Between Community Structure and Habitat Descriptors

The first screening tool used to assess the degree of association between the benthic community and habitat descriptors was Mantel's test. Mantel's test tested for concordance between patterns in the benthos community and patterns in the various habitat descriptors, both within each year-depth combination and for both years and depths combined. Six groups of habitat descriptors were considered relevant: (1) depth (5 and 20 m); (2) type of substratum (coded numerically; 1 = bedrock, boulder, cobble; 2 = gravel; 3 = sand; 4 = silt; 5 = clay); (3) transect location; (4) fetch (matrix of the unobstructed distances to shore in each of eight compass directions); (5) upwelling (distance to the 50 m depth contour); and (6) percentage cover and thickness of Cladophora. All habitat-based distance matrices were based on Euclidean distances. Substrate codes were based on descriptions of surface veneer by the same divers that collected the samples (Integrated Explorations, 1992). Given the coding scheme for the substrate categories, we inherently assumed that communities associated with bedrock, boulder and cobble were as different from gravel as they were from silt and clay. A significant correlation using this analysis would corroborate that suggestion while a lack of a correlation would not suggest a lack of substrate-related variation in community structure. As a result, we also used ANOVA to test for differences in CA axis scores between substrate classes.

For the benthic community, Chi-Square distances between samples were calculated. This distance measure was chosen because it would complement summaries based on

Correspondence Analysis and TWINSPAN. Both of these techniques begin with a Chi-Square distance matrix.

When Mantel's test detected significant correlations between the community and habitat distance matrices, the nature of the correlations was explored by plotting CA axis scores, and by examining TWINSPAN maps and tables. Some of the follow-up analyses were complex and are described in the results section to improve clarity. In part to provide a summary of the detailed taxonomic work that was conducted, we also performed TWINSPAN on the 1991 data set using detailed species-level identifications. This more detailed TWINSPAN was used to assist in identifying spatial trends from the 1991 survey. We did not analyze differences in community composition between 1981 and 1991 using species-level taxonomy because of uncertainties in matching the 1981 and 1991 species lists (Table 2).

Effect of Zebra Mussels on Community Structure

Zebra mussels were found at Transects 1-5, 7-9, 18 and 24 at 5 m. At 20 m, they were found less frequently. We used two methods to determine if zebra mussels were related to variations in community structure in Lake Ontario. First, we contrasted changes in community structure where mussels were found, with changes where mussels were not found (at 5 m). This was tested using the ANOVA model give in Table 5. If there were different changes in community composition at infested locations than at uninfested locations between 1981 and 1991, the ANOVA would result in a significant *Year·Infested* interaction term. The model in Table 5 follows from Green's (1979) BACI (before-after control-impact) design. We used axis scores from CA as our descriptors of community structure.

The second line of evidence for (no) effects of zebra mussels came from examination of TWINSPAN tables and maps based on major taxonomic groups, and the second TWINSPAN based on detailed taxonomy. For this specific question, the more detailed TWINSPAN was somewhat more sensitive for detecting alterations in the benthic community that might be attributable to zebra mussels (see results).

2.3.3 Analysis of Macro-Scale (Bivalve) Benthos Data

As outlined in the description of field methods, a separate group of samples was collected specifically for the purpose of testing for effects of zebra mussels on densities of sphaeriid clams and unionids. In total, 40 samples of sphaeriids and dreissenids were collected from eight locations at 5 m (Transects 1-5, 7-9). We were also interested in describing size class distributions with the intent of establishing the timing of first settlement in Lake Ontario. The two sections that follow describe the specific methods used to analyze those data.

2.3.3.1 Assessing the Associations Among Bivalve Taxa

Correspondence Analysis (CA) was used to summarize and illustrate the associations among the 17 bivalve taxa collected and among sample locations, as part of the macro-scale bivalve sampling. CA was conducted using the raw data. The first three CA axes were retained and bivariate plots of the taxa and sample CA scores made. Taxa were considered important to the structure of the CA axes if they had contributions to the CA axes of > 10% and had squared correlations with the axes of > 0.50. These values were selected arbitrarily through trial and error, with the objective of providing sensible interpretations. If zebra mussels were having influences on the composition of the sphaeriid fauna, the structure of CA axes would have been at least in part influenced by zebra mussels. For example, if zebra mussels were resonsible for increases or decreases in numbers of specific sphaeriids, those sphaeriids and zebra mussels would have contributed to and been related to a common CA axis.

2.3.3.2 Describing Population Structure

To illustrate variations in size class structure, we plotted length frequency histograms for each population of zebra mussels.

3.0 RESULTS

3.1 Habitat Descriptions

Substrate type was generally similar at sites between 1981 and 1991, with some exceptions (Table 6). In some cases substrates were classified finer in 1991 than in 1981 (e.g., 20 m, Transects 2-4), whereas, in other cases, substrates were classified as coarser in 1991 than in 1981 (e.g., 20 m, Transects 8, 18, 22). Generally, if substrates were classified as different at one depth of a transect from 1981 to 1991, the other depth at the same transect was classified the same in both years. Substrate differences between years were more likely due to variability in positioning in association with heterogeneity in substrate composition along transects rather than habitat modification.

Considering the shoreline as a whole, the occurrence of Cladophora may have declined between 1981 and 1991 (Table 7). With the exception of stations 1-5 in the western end of the lake, the occurrence and percent coverage in 1991 was generally lower than in 1981. Cladophora was present at Transects 21-23 in 1981 but was absent in 1991. Also, during 1981 Cladophora was absent at Transects 2-5, but was present in 1991.

3.2 Meio-Benthic Communities

Between 1981 and 1991, there were general changes in composition of the benthic community at both 5 and 20 m. Most of the changes reflected improved water quality. Some habitat features were shown to be related to the composition of the benthic community, but only depth had a consistent effect in both 1981 and 1991. The sections that follow describe the differences in composition between 1981 and 1991 at each of 5 and 20 m and among locations in the lake. They also describe the nature of the relationships between benthic community composition and habitat descriptors, discuss the power of the survey for detecting year to year changes and show that zebra mussels have had little effect on the rest of the community.

3.2.1 Temporal Changes in Community Structure, 1981 to 1991

General changes in community structure between 1981 and 1991 were different at 5 and 20 m. At 5 m, the benthic community in 1991 had a higher percent composition of gastropods and amphipods with a lower percent composition of naidids and tubificids. At 20 m, lumbriculids were more important to the benthic community in 1991 than they were in 1981, while the percent composition of chironomini and naidids was reduced in 1991. Other more specific changes in community structure were also evident and depended on depth and location in the lake. Of particular interest were the increased occurrences of mayflies along the north shore at 5 m, and a reduction in the numbers of chironomids between Niagara-on-the-Lake and Hamilton at 20 m.

Our analysis of changes between 1981 and 1991 included four approaches. First we used ANOVA to test for changes in abundances of 17 major taxonmic groups and three indices. Second, we ordinated the major taxon abundances using Correspondence Analysis. Third, we used TWINSPAN to cluster the stations and taxa into groups. Fourth, we examined histograms of taxa abundances.

Sixteen of the 17 major taxonomic groups (all but the Diamesinae) and the three summary indices (Richness, Shannon's H', Total Abundance) exhibited complex variations. Specifically, each of these groups and indices exhibited changes between 1981 and 1991 which depended on where they were collected and the depth they were collected from (Table 4; Figures 2-19). At any given location, it was difficult to predict the nature of the change at 20 m given the nature of the change at 5 m. For example, histograms of taxa richness show that at Transect 24 (Prince Edwards Bay) the number of species increased at 5 m and decreased at 20 m, whereas at Transect 6 (Hamilton Beach) the number of species at 5 m did not change but was lower at 20 m. Numbers of Tanytarsini are also a good example of this interaction. At 5 m, numbers of Tanytarsini increased at some stations between Niagara and Hamilton, but decreased at others. At 20 m, Tanytarsini were missing between Niagara and Hamilton but increased at other stations at 20 m (Figure 16).

The presence of these three-way interactions provided evidence that the sampling design (3 replicates, 2 depths, 25 transects) was adequate to detect changes in the composition of Lake Ontario benthos between years. However, variations in numbers were greater for some groups and are therefore more easily detected than other groups. With 25 transects, detectable effects sizes varied between 168 m^{-2} (polychaetes) to 40,407 m^{-2} (tubificids). However, compared to the grand mean densities, effect sizes ranged from 3.17x the mean for amphipods to 13.6x the mean for Ephemeroptera. The average effect size for all taxa was 5.8x the mean (Appendix D). Relative effect sizes tended to be smaller with taxa that were dominant members of the community. For example, numbers of amphipods which comprised about 19% of the total numbers in both 1981 and 1991 would only need to change by ≈ 5x for a change to be detected using 25 transects. In contrast, changes in densities of Ephemeroptera, which accounted for < 1% of the total numbers would have to change by over 13x before they would be detected with 25 transects (Appendix D). Consequently, future changes in benthic community structure may be more easily detected by summarizing patterns of variation in the dominant groups.

Detection of changes in community composition is usually more sensitive when multivariate approaches are used (Warwick et al., 1988; Gray et al., 1988). Our multivariate analyses included ordination by Correspondence Analysis and TWINSPAN. These analyses showed that there were general differences between 1981 and 1991 communities at 5 and 20 m.

The taxa important to the structure of the CA axes are given in Table 9. The first CA axis described a gradient of increasing to decreasing dominance of gastropods and amphipods, and decreasing to increasing dominance of naidids and tubificids. Gastropods and amphipods are mainly shallow-water organisms. Figures 20 and 21 show that the first CA axis contrasts the 1981 and 1991 5-m communities such that the 1991 community had a higher percent composition of amphipods and gastropods. A t-test of the changes in CA axis scores between 1981 and 1991 confirmed that this axis separated 1981 and 1991 at 5 m (Table 8). The second CA axis described a gradient of increasing to decreasing composition of chironmini and naidids, and decreasing to increasing composition of lumbriculids. This second axis contrasted the 20-m communities in 1981 (higher composition of chironomini and naidids) and 1991 (higher composition of lumbriculids) (cf Table 8, Figures 20, 21). The second axis also contrasted 5 and 20 m communities in 1981 (Figures 20, 21). The third CA axis described a gradient of increasing to decreasing composition of tanytarsini and chironomini, and decreasing to increasing composition of gastropods. This third axis primarily contrasted 5 and 20-m communities with a higher percent composition of gastropods at 5 m, and a higher percent composition of tanytarsini and chironomini at 20 m. A t-test showed that this third axis could also be used to separate 1981 and 1991 20-m communities (Table 8), suggesting a higher number of gastropods in 1981 at 20 m. However, Figure 17 shows that numbers of gastropods were higher in 1991 confirming that this axis primarily separated 5 and 20 m communities in both 1981 and 1991.

The compositional differences detected by CA were also illustrated in Figures 22 and 23. Both histograms show the direction and magnitude of change in CA axis scores between 1981 and 1991 at 5 and 20 m at each transect. At 5 m (Figure 22), it was evident that these changes were prevalent from Transects 1-23. The major-groups TWINSPAN was also used to illustrate changes in composition of the benthic community between 1981 and 1991 (Table 10). To contrast years at each of 5 and 20 m, groupings from the TWINSPAN table can be compared. Groups 1 and 2 represented 5 m samples and could be used to contrast 1981 (Group 1) and 1991 (Group 2). Group 1 samples in 1981 were collected at various stations around the lake (Figure 24) and were dominated by naidids, amphipods and gastropods. However, these samples were by no means representative of the average 5-m station in 1981 (Figure 24). In general, the average community described by TWINSPAN at 5 m in 1981 was Group 4, which was more dominated by naidids and tubificids (Table 10) and tended to be collected between Hamilton and Port Hope. Group 4 was also dominant at 20 m suggesting some similarity between the 5 and 20 m stations in 1981. This was consistent with the results from CA which shows the 1981 5-m samples to be more similar to the 20-m samples from both 1981 and 1991 (Figure 20). Group 2 samples (1991) were dominated by gastropods, naidids and amphipods and were found throughout most parts of the lake in 1991 (Figure 25). Group 2 was the most diverse of those groups described with richness per site averaging 44 taxa (other groups averaged < 30 taxa; Table 10). Ephemeroptera were also members of this group.

At 20 m, 1981 communities were also dominated by TWINSPAN group 4. This community was prevalent in both 5 and 20 m depths and was suggestive of poorer water quality than any of the other groupings identified by TWINSPAN (Table 10). With the 1991 data, TWINSPAN identified 20-m samples as belonging predominantly to groups 7 and 8 (Figure 25). Both groups 7 and 8 were dominated by gastropods, sphaeriids, lumbriculids and tubificids. An additional change, which was obvious only after inspection of density histograms, was a reduction in the prevalence of chironomids between Niagara-on-the-Lake (Transect 1) and Etobicoke (Transect 9) (Figures 12-16).

3.2.2 Concordance Between Community Structure and Habitat Descriptors

To evaluate the association between habitat descriptors and community composition, we first tested for concordance between distance matrices based on the habitat descriptors, and distance matrices based on community composition using Mantel's test. According to those first initial screening tests, community structure in Lake Ontario was related to depth, fetch (particularly in 1991), upwelling (1981, 5 m; 1991, 20 m), and substrate (1981, 20 m) (Table 11). Each of these effects was further examined by analysis of CA axis scores and through assessment of the TWINSPAN groupings. The results of the more detailed analyses are described in the sections below.

3.2.2.1 Differences Between 5 and 20 m Communities

There were general differences in community structure between 5 and 20 m common to both 1981 and 1991 which included a higher proportion of gastropods at 5 m, and a higher proportion of chironomids (Tanytarsini, Chironomini) at 20 m. However, differences were more pronounced during 1991 than in 1981. For example, in 1981, both the 5 and 20 m communities were highly dominated by oligochaete worms. In 1991, a reduction in the number of naidids and tubificids at 5 m resulted in the 5-m community being more dominated by amphipods and gastropods.

Differences in composition of the benthic communities at 5 and 20 m in both 1981 and 1991 can be inferred from examination of plots of CA axis scores (Figure 20) and through examination of the major-groups TWINSPAN (Table 10, Figures 24, 25). Correspondence Analysis separated 5 and 20-m communities along axis 3 suggesting a higher proportion of gastropods at 5 m and a higher proportion of chironomids at 20 m. The TWINSPAN groupings (Table 10) directly separate 5 and 20-m communities with groups 1-3 principally representing 5-m communities and groups 4-8 principally representing 20-m communities. TWINSPAN suggested the 20-m communities had higher proportions of sphaeriids and oligochaetes, while the 5-m communities had higher proportions of gastropods, chironomids, caddisflies (Trichoptera) and mayflies (Ephemeroptera) in 1991. With the exception of the mayflies, these patterns were consistent in both 1981 and 1991.

3.2.2.2 Variation Among Substrate Classes

There was little evidence of a strong substrate-related effect on the benthic community in either 1981 or 1991 at 5 and 20 m. Three different analyses were used to test for substrate effects; (1) Mantel's test, (2) ANOVA on CA axis scores, and (3) subjective assessment of the relationship between TWINSPAN groupings and substrate classifications. These approaches did not detect strong substrate effects, and those effects detected were weak and inconsistent.

Mantel's test suggested a significant relationship between substrate classes when coded on a scale of 1-5 with the coarsest substrates (bedrock, boulder, rock) coded 1 and clay coded 5. This correlation was present at 20 m in 1981 only. The presence of this correlation suggests that community structure was more similar between rock and gravel than it was between rock and clay. However, as discussed in the methods section, coding substrates 1-5 infers that we expect communities on boulder to be more similar to communities on gravel than on clay: Mantel's test treated our substrate coding as a continous variable. Communities on boulder may have been as different from those on gravel as they were from those on clay. Consequently, in addition to the Mantel's test, we used ANOVA to determine if there were differences in CA axis scores (i.e., community composition) among substrates within years. The results of those ANOVAs are given in Table 12. In general, there was little evidence of strong substrate-related variation. The relationship suggested by Mantel's test at 20 m in 1981 was not significant when the ANOVA approach was used on the CA axis scores (Table 12). The ANOVAs did suggest that CA axis 1 scores varied with substrate type at 20 m in 1991 with silt and clay having apparently higher proportions of gastropods and amphipods than sand and boulder which had higher proportions of naidids and tubificids. Figure 26 gives box plots of average CA axis scores for each substrate class and illustrates the lack of strong substrate-related variations in community structure within depth and year combinations.

Finally, none of the TWINSPAN groupings (Table 10) were obviously related to substrate type. This provides more evidence to suggest that substrate-related phenomena were negligible in relation to the other factors causing variation in the benthic fauna in Lake Ontario.

3.2.2.3 Variation Among Locations

The variety of analyses conducted suggested that there were specific geographic patterns to variation in the benthic community. The dominant regional patterns included a large cluster of communities suggestive of richer nutrient conditions then elsewhere along the north shore at 5 and 20 m in 1981. In 1991 at 20 m, there was a cluster of enriched communities near Toronto and Quinte. At 5 m in 1991, there were four distinct communities detected using species-level clustering (TWINSPAN): (1) between Niagara and Hamilton the community was dominated by amphipods and gastropods; (2) along the north shore and (3) at the east end of the lake the community had high richness and low dominance by tubificids; and (4) near Toronto the community (mainly naidids) was more indicative of enriched conditions relative to the other stations. These patterns were elucidated by first testing for a regional effect with Mantel's test, illustration of the patterns by plotting CA axis scores and labelling the transects (Figures 27, 28), and by interpretation of the TWINPAN major groups and species-level groupings.

Mantel's test detected significant correlations between station proximity (or distance) and community structure suggesting that communities closer together were more similar. This pattern was detected for the whole community and for the communities at 5 m in 1981 and 20 m in 1991. At 5 m in 1981, both CA and TWINSPAN group samples from Transects 22, 24 and 25 with samples from Transects 1 and 2 (cf Table 10, Figure 27). In 1981, the most obvious pattern was a large cluster of group 4 communities along the north shore of the lake and west of Toronto at both 5 and 20 m (Figure 24). As discussed before, those group-4 communities were dominated by naidids and tubificids and were suggestive of poorer water quality in relation to the other groups present at the time.

In 1991, the major-groups TWINSPAN showed distinct groupings of communities at 20 m only. Most of the 20-m communities were group 7, while there were patches of group-5 communities near Toronto and Quinte. As before, those group-7 communities were dominated by naidids, lumbriculids and sphaeriids, with low numbers of chironomids (especially between Niagara and Hamilton). The group-5 communities near Toronto and Quinte were dominated by naidids, isopods, amphipods, sphaeriids and tubificids. In contrast to the group-7 communities, the group-5 communities were probably evidence of enriched conditions near Toronto and Quinte.

The detailed species-level TWINSPAN (Table 13, Figure 29) was more successful at identifying particular groupings of stations at 5 m which had some apparent geographical orientation. At 5 m, there were four distinct groups of samples:

(1) Group 1 between Niagara and Hamilton,
(2) Group 2 between Transect 17 (Cobourg) and Transect 25 (Amherst Island),
(3) Group 3 along the north shore of the lake, and,
(4) Group 6 near Toronto.

Of these groupings, Group 6 communities near Toronto were dominated by organisms more typical of poorer water quality (mainly tubificids). In contrast, Group 2 and 3 communities from the east end of the lake and the north shore respectively had a wider variety of organisms and were less dominated by tubificid worms. Group 1 communities between Niagara and Hamilton were dominated by amphipods and gastropods.

3.2.2.4 The Effects of Fetch

In 1991 at both 5 and 20 m, community structure was related to measures of fetch. However, there was a lack of similarity in the nature of the relationships at 5 and 20 m making it difficult to infer that fetch *per se* was responsible for the observed relationships. To assess the effects of fetch, we first used Mantel's test to determine if community composition and measures of fetch (unobstructed distance to shore in each of eight compass directions) were related. We then determined how fetch varied among transects in the lake by ordinating the fetch measures. Finally, we compared TWINSPAN groupings and CA axis scores among four exposure zones in the lake.

Mantel's test detected significant correlation between the community and fetch distance matrices for the whole community (both dates and depths), and for 5 and 20 m in 1991 (Table 11). To explore how the community was related to fetch, it was first necessary to summarize the fetch measures (distances to shore in each of eight compass directions) in a reduced space. For this purpose, non-metric multidimensional scaling was used to ordinate a Euclidean distance matrix (Wilkinson, 1990) based on distances in the eight compass directions. The MDS ordination is summarized in Figure 30 which gives the axis scores for each station location. Also overlain on these two graphs are the correlations between the original eight distances and the MDS axis scores. These graphs essentially re-create the geographic positioning of the sampling stations. For example, on the 5-m graph, stations to the left of the graph were in the west end of the lake and had long easterly fetches; stations at the top of the graph were on the north shore of the lake and had long southerly fetches; and stations to the right of the graph were from the west end of the lake and had long westerly fetches.

From Figure 30, we can discern three basic zones of exposure:

(1) Transects 1-6 (between the Niagara River and Hamilton) which were more exposed in a northerly direction than other transects;

(2) Transects 7-9, 11-14 (Bronte to Whitby) which were more exposed in an easterly direction than other transects; and,

(3) Transects 10, 15-25 (Newcastle to Ostrander Point) which were more exposed in a southerly or southwesterly direction than other transects.

Note that Transect 10 had a short north-easterly fetch and clustered with the transects from the east end of the lake.

To determine the nature of the relationship between community structure and fetch in 1991 we used two different approaches. First we examined TWINSPAN maps and tables based on both the major groups and detailed taxonomy for 1991. Neither of the TWINSPAN analyses produced groupings in 1991 at 5 or 20 m that matched with the exposure groups. The second analysis involved using ANOVAs to test for differences in CA axis scores between exposure groups. Some differences were found (Table 14) and box plots of exposure group observations were made to illustrate the major differences (Figure 31).

At 5 m, there were differences in CA axis 1 and 2 scores among exposure groups while at 20 m there were differences in CA axis 2 scores only (cf Table 14 and Figure 31). Figure 31 shows that at 5 m, stations with a long southerly fetch had lower CA axis 1 scores and higher CA axis 2 scores than the other stations. This suggests that communities exposed to long southerly fetches had communities in which naidids, chironomids and lumbriculids were important while amphipods and gastropods were less important.

At 20 m, CA axis 2 scores were lowest for stations along the eastern end of the lake with a long westerly fetch and higher for stations along the south side of the lake with a long northerly fetch (cf Table 14 and Figure 31). Numbers of chironomini and naidids were higher, and lumbriculids lower at stations from the south side of the lake with long northerly fetches. In contrast, stations from the east end of the lake with long westerly fetches had lower numbers of chironomini and naidids with higher numbers of lumbriculids.

3.2.2.5 Effects of Upwelling

Upwelling was measured as the distance from the sampling station to the 50 m contour. To determine if upwelling was related to community structure we first used Mantel's test. Mantels's test detected an association between community structure and likelihood of upwelling in 1981 at 5 m and in 1991 at 20 m (Table 11). To explore the nature of the association, we plotted CA axis scores vs distance to the 50 m contour (our measure of likelihood of upwelling). Stations at Transects 24 and 25 were far from the 50 m contour and tended to have communities somewhat deviant from the remainder of the stations in both 1981 (5 m) and 1991 (20 m) (Figures 32 and 33). These stations were largely responsible for the observed relationships between upwelling and community composition. Communities closest to the 50-m contour were those on the north shore of the lake. At 5 m in 1981 those communities on the north shore had low CA axis 1 scores and high CA axis 2 scores suggesting dominance by naidids and tubificids, with gastropods, chironomids and amphipods of less importance. TWINSPAN identified those stations as having Group 4 communities (Figure 24). At 20 m in 1991, communities along the north shore of the lake had high CA axis 3 scores suggesting that chironomini and tanytarsini were important while gastropods were less important to the community. Again, the major-groups TWINSPAN tended to group the northern shore communities together (Figure 25).

3.2.2.6 Effects of Zebra Mussels

At the major-group level, there was no obvious effect of zebra mussels on community composition. However, at the species level, zebra mussels appear to have altered the composition of the community between Niagara and Hamilton, particularly the dominance of species within the gastropod community.

To determine if zebra mussels had an effect on community composition at the major group level, we tested for differences in changes in CA axis scores between infested and uninfested locations. The lack of significant interaction in the ANOVA models suggested that there were no differences in the changes in community measures (the three CA axes) between 1981 and 1991 in infested an uninfested stations. However, that analysis assumes that the mere presence of zebra mussels would be important to community structure. It may be that where zebra mussels are only sparsely found (e.g. Transect 18 at Presquile and Transect 24 at Prince Edward Bay, see histogram Figure 19) there is negligible change in the rest of the benthic fauna. Along the Niagara-Hamilton corridor where zebra mussels were most abundant, changes to overlying water quality due to zebra mussels may cause more dramatic shifts in the remainder of the community. TWINSPAN tables based on major groups tended to group the 5 m stations in the Niagar-Hamilton corridor with other stations around the lake suggesting no effect. However, TWINSPAN based on the detailed taxonomy grouped the Niagara-Hamilton 5-m stations by themselves suggesting a possible impact. Those 5-m stations along the Niagara-Hamilton corridor were dominated by Pleurocera acuta, Gammarus fasciatus, Physella gyrina and Stylaria lacustris. Other 5-m stations in 1991 were dominated by Probythinella lacustris, G. fasciatus, P. gyrina, and Hyalella azteca. Along the Niagara-Hamilton corridor, the average number of taxa per sample was lower than at other 5-m stations, reflecting a higher number of insect taxa (chironomids, and aquatic mites) in other areas (Table 13).

3.3 Macro-Scale (Bivalve) Communities

3.3.1 Associations Among Bivalve Taxa

The average numbers of bivalves from each of the main bivalve families are presented in Table 15 (raw data are given in Appendix F). Zebra mussels were found at eight of the 25 transects (1, 2, 3, 4, 5, 7, 8, 9) with highest densities at Transects 1 and 2. One unionid was found at Transect 4. Sphaeriids were collected at all but Transects 5 and 8, and were collected in highest numbers at Transect 4 (Table 15).

Ordination Patterns

Sphaerium nitidum and Pisidium fallax were important to the structure of the first CA axis, whereas Sphaerium striatinum, Pisidium lilljeborgi, and Unionidae were important to the second axis, and Musculium transversum was important to the third axis (Table 16; detailed summaries of the CA are provided in Appendix G). Bivariate plots of the three CA axes are provided in Figures 34 and 35. Samples from Transect 4 were separated from samples at other Transects primarily because of variation in CA axis 1 scores, or because of variation in densities of P. fallax and S. nitidum. Mantel's test indicated that a distance matrice based on the abundances of zebra mussels and distance matrix based on abundances of sphaeriids (Musculium, Sphaerium, Pisidium) were not associated (r = 0.181; p = 0.44). This confirmed that the distribution of sphaeriids and unionids was not correlated or associated with the distribution of zebra mussels.

3.3.2 Population Structure

At less than half of the transects where macro-scale sampling was conducted, zebra mussels had three size classes (Niagara-on-the-Lake, Port Dalhousie, Jordan Harbour, Stoney Creek) (Figure 36). In those cases, the smallest size class was less than 5 mm long, the second was between 10 and 15 mm, and the third size class was greater than 20 mm. When two size classes were found (Beamsville, Bronte, Oakville, Etobicoke) the first size class was usually less than 5 mm long whereas the second size class varied between 14 and 21 mm. The average shell length of the dominant size class at each transect increased from Transect 1 (Niagara) to Transect 9 (Etobicoke) (Figure 36).

4.0 DISCUSSION

Variation in benthic community structure in Lake Ontario at 5 and 20 m in 1981 and 1991 was difficult to relate to naturally occurring environmental conditions such as fetch, likelihood of upwelling, substrate or Cladophora. Most of the observed variation, was more easily attributed to temporal and spatial differences in water quality, and was suggestive of fairly substantive improvements in water quality over the 10-year period. Changes in water quality were more obvious from the 5 m communities than they were from the 20 m communities. At 20 m, communities along the north shore of the lake exhibited substantial improvements, while those between Niagara and Hamilton exhibited changes which deserve further attention due to their nature. The presence of zebra mussels at 5 m between Niagara and Hamilton may have caused changes in species-level composition, but if so, has not altered the overall function of the community. These statements are discussed in more detail below.

4.1 Influence of Natural Environmental Variables

Although there were various significant relationships between community structure and the environmental parameters described, the nature of the observed relationships makes it difficult to directly attribute cause and effect.

Upwelling

For example, the relationship between upwelling and community structure was driven by Transects 24 and 25, and the relationship was only obvious at 5 m in 1981 and 20 m in 1991. If upwelling had been the cause of deviation of the 5-m communities at Transects 24 and 25 from the remainder of the 5-m communities, then we would have expected to see a similar pattern in 1991 when the influences of water quality should have been less pronounced. Barton (1986) suggested that the lack of insects along the north shore in 1981 was probably due to upwelling events bringing cold water to those communities and making it unlikely that insect life histories could be completed. Given the presence of Ephemeroptera along the north shore in 1991, it is difficult to suggest that thermal regimes were the cause of the observed patterns in 1981. In addition, the communities from Transects 24 and 25 may have been deviant from the other communities for a variety of reasons un-related to upwelling. For example, they are from the shallowest part of the lake where thermal regimes unrelated to upwelling are different than in other parts of the lake (Gachter et al., 1974) and which may receive more allochthonous energy from the Bay of Quinte (Johnson and Brinkhurst, 1971) than other stations might from other sources. Removing those two stations from the analysis would undoubtedly have eliminated any strong relationship with upwelling. In relation to the other Great Lakes, upwelling events in Lake Ontario may cause the nearshore zone benthos to be depauperate of some groups of organisms, but upwelling does not appear to be a strong determinant of community structure within Lake Ontario.

Substrate & Cladophora

The lack of strong association between community structure and variables such as Cladophora and substrate, two variables which are known to cause variation in benthic communities, makes it obvious that other factors (possibly local water quality) are overriding their influences. The observed variations in community composition from place to place were more easily attributable to expected spatial patterns in water quality then the influences of substrate texture and Cladophora. Since water quality variation across the study area was not examined, the suggested association between spatial pattern of composition and water quality is speculative.

In part, our inability to detect correlations between community structure and factors such as substrate, was due to not collecting communities from different substrates within locations. When Integrated Explorations (1984) conducted the 1981 survey, they did collect samples from different substrates within stations. Barton's (1986) analysis of those data did detect significant correlations between community structure and substrate, suggesting that in Lake Ontario and at the depths we studied, substrate does influence the composition of the community. However, the fact that we did not detect a strong substrate or Cladophora effects suggests that water quality, or other station-specific factors, overrode the influences of substrate texture during the 1991 survey.

Fetch

There was a lack of concordance between the nature of the observed relationships between fetch and community structure at 5 and 20 m making it difficult to interpret the patterns. Long fetch infers exposure to prevailing winds and more turbulent shore zones. It has been attributed with causing variation in shell etching of unionids along shore zones of acidified lakes (Hinch and Bailey, 1988), and variations in species richness of molluscs along the shores of Lake Erie (Bailey, 1988). Fetch is more likely to cause greater variation in shallower water because it generally increases water turbulence. In addition, we would expect that stations at opposite ends of a fetch gradient (for example at either end of the east-west fetch in Lake Ontario) would respond in similar manners. That communities exposed to long southerly and northerly fetches did not have similar composition at either 5 or 20 m suggests that fetch was not responsible for the observed patterns. More likely, the observed correlation was due to spatial variations in water quality.

Depth

The only environmental factor which could be specifically attributed with causing variation in the benthic community in this study was depth. Communities from 5 and 20 m were consistently different with 5 m communities having higher taxonomic richness, more chironomids and other insects, and more gastropods than the 20-m stations. Both 5 and 20 m stations had high numbers of naidids, tubificids, and amphipods but 20 m stations tended to have more sphaeriids and lumbriculids (Table 10; Figures 20, 21). The depth-related variations observed in this study are consistent with observations from other studies (Johnson and Matheson, 1968; Johnson and Brinkhurst, 1971; Kinney, 1972; Barton and Griffiths, 1984; Barton, 1988). The general depth-related pattern was a shift from epibenthic organisms (insects, gastropods) that would tend to live on top of the rock that predominated at 5 m, to infaunal organisms (lumbriculids, sphaeriids) that would tend to live in the finer substrates that were more dominant at 20 m. Oligochaete worms have historically been shown to increase in numbers with depth in association with finer substrate (Johnson and Matheson, 1968), whereas chironomids have historically been more abundant in the shallower waters (Johnson and Brinkhurst, 1971). Insect taxa tend to be less prevalent in deep-water stations because they of need to be closer to shore for completion of reproductive cycles (Barton and Smith, 1984). Gastropods are also expected to be more dominant at 5 m where light is more likely to penetrate and result in growth of periphytic food.

Although the differences in communities were generally consistent in both years, the changes in community composition from 1981 to 1991 were quite different at each depth. Consequently, they are discussed separately in the next section.

4.2 Temporal Changes in Community Structure, 1981 to 1991

5 m

With the exception of a few transects, variation in community structure between 1981 and 1991 suggested that there had been improvements in water quality, particularly at 5 m, and particularly between Hamilton and Toronto and along the north shore of the lake (Figures 24, 25). The general pattern of change at 5 m was an increase in richness and diversity values, increased densities of most major groups (particularly gastropods, and amphipods), and reductions in numbers of taxa generally associated with degraded water quality (i.e., naidids and tubificids; Cook and Johnson, 1974). At 5 m the increased prevalence of Ephemeroptera, although contribution to total numbers was low, was also a significant finding.

Increases in richness and Shannon's H' may have been due to small differences in sampling strategies between 1981 and 1991. The data analyzed from the 1981 survey included only samples collected during July. The 1991 survey was conducted during mid to late August at which time there might have been naturally higher diversity of fauna than samples collected in July. Benthic samples typically have a more diverse community and higher number of taxa in late fall because most insect groups will be present at least as early instar larvae preparing for overwintering (Plafkin et al., 1989; Anderson, 1990).

Although worm taxa will exhibit some degree of fluctuation in numbers with season (e.g., Poddubnaya, 1980), there is little evidence that dominance patterns of oligochaetes changes seasonally (Brinkhurst, 1969). To determine if seasonality may have contributed to the differences in numbers of worms between 1981 and 1991, seasonal data from the 1981 survey were analyzed to test for seasonal changes in worm abundances (Appendix H). The analysis did not clarify whether the latter period of sampling in 1991 than in 1981 could account for the observed differences in composition. In the analysis (Appendix H), it was clear that at at least some sites, the estimates of many of the taxon abundances changed strongly over time, but the direction of the changes and the magnitude of the changes were not consistent among stations. Given this, the interpretation of the changes in abundances of worm taxa between the extensive surveys in 1981 and 1991 should be made cautiously.

Changes in numbers of gastropods probably did not reflect seasonal differences in sampling since these groups tend to produce young during the spring (Servos et al., 1985) and young would be large enough to be retained by sieves during collection in later summer or early fall. Gastropods tend to increase in numbers when water clarity improves and either aquatic macrophytes are allowed to grow, or there is a periphytic food resource (Mackie and Qadri, 1973; Griffiths, 1993). Consequently, changes in the numbers of gastropods possibly provides more evidence, than some of the other groups, that water quality in the lake (at 5 m) had improved.

20 m

At 20 m, there was a significant change in community structure, which was also suggestive of a general improvement in water quality, particularly along the north shore: the major change was a reduction in numbers of tubificids and naidids with increases in numbers of lumbriculids, gastropods and sphaeriids. The change in community structure along the north shore was likely due to a change in water quality, but as discussed above, this conclusion is tempered by the slightly different sampling periods between the 1981 and 1991 surveys.

The reduction in numbers of chironomids between Niagara and Hamilton at 20 m is interesting and difficult to explain. Given the improvements in water quality throughout the lake, it would be reasonable to expect numbers of chironomids to either remain the same or increase. A reduction in numbers of this group suggests an impact unrelated to the usual enrichment scenario. In this region of the lake, the greatest single change is the presence of zebra mussels. However, they were only found in large numbers at 5 m, where chironomids were quite common. The lack of chironomids along this part of the lake is somewhat startling and deserves further attention. They are usually tolerant to most disturbances being replaced only when enrichment and oxygen demands are extreme.

4.3 Influences of Zebra Mussels on Community Structure

There appears to have been a significant yet subtle effect of zebra mussels on the benthic community between Niagara and Hamilton where zebra mussels were most prevalent. The effect of zebra mussels was evident only when considering species-level taxonomy. Using major-groups taxonomy, TWINSPAN was unable to discriminate between communities with and without zebra mussels. The most obvious differences between the communities with and without zebra mussels was a lower number of taxa probably driven by a reduced number of chironomid and aquatic mite taxa. Other differences included higher numbers of most snails, particularly Valvata tricarinata, Physella gyrina and Pleurocera acuta in communities with zebra mussels. In those without mussels Probythinella lacustris and P. gyrina were dominant members of the snail community. This increase in numbers of snails is similar to changes observed in Lake St. Clair by Griffiths (1993) who attributed that change to improved water clarity followed by growth of aquatic macrophytes, and in Lake Erie by Dermott et al. (1993). The increased prevelance of Cladophora between Niagara and Hamilton may have been caused by increased water clarity and may have caused the sublte shifts in community structure that were observed. Increased water clarity along the Niagara-Hamilton corridor could have resulted from the filtering activities of the zebra mussel populations along that section of the lake, or from clearer waters coming into Lake Ontario from Lake Erie.

4.4 Zebra Mussels & Other Bivalves

4.4.1 Associations Among Bivalve Taxa

Associations between zebra mussels and other bivalve taxa from transects that had zebra mussels suggest that there were no negative or positive effects of zebra mussels on other bivalve taxa. Samples from Transect 4 (Beamsville) appeared to be different than all of the other bivalve samples collected in western Lake Ontario. High numbers of specific sphaeriids (S. nitidum and P. fallax) appeared to be responsible for the separation of samples. This general pattern of no substantial change in numbers of sphaeriids is not in agreement with the conclusions from the meio-scale benthic survey (Section 4.3.1) for the whole lake (Canadian side). The meio-scale survey showed that in the Niagara region where the zebra mussel has colonized, numbers of sphaeriids increased somewhat at 5, but particularly at 20 m. This general pattern also agrees with results from Lake Erie where Dermott (1993) showed that numbers of sphaeriids increased substantially in the presence of zebra mussels.

The lack of effects in the macro-scale survey may suggest that the range in densities of zebra mussels at the time of the survey was not large enough to have any more influence than the simple presence of mussels. Abundances of mussels during this survey were quite low (<25,000 m^{-2}) compared to what numbers could potentially have been (>400,000, MacIsaac et al., 1991). In addition, the numbers of sphaeriids collected as part of the macro-scale survey were much lower (0-195 m^{-2}) than those collected as part of the meio-scale survey (>3,600 m^{-2}) in the Niagara region (cf Figure 20, Table 13). This suggests that sampling methods used to collect zebra mussels and sphaeriids underestimated numbers of sphaeriids. Consequently, some caution should be used when considering the results and interpretations associated with the macro-scale survey.

4.4.2 Population Structure

Density of zebra mussels in the western end of Lake Ontario during 1991 varied between 611 m^{-2} at Transect 7, to over 24,000 m^{-2} at Transect 1 (Figure 19). These numbers are lower than population estimates for zebra mussels from Lake Erie (e.g., Dermott et al., 1993), but are similar to population estimates from Lake St. Clair (Griffiths, 1993). There were at least two length classes of mussels at each site with size of the largest length class between 18 and 22 mm (Figure 36). Mackie (1993) has suggested that zebra mussels in Lake St. Clair can grow to at least 20 mm within one year. If it is assumed that the mussels in Lake Ontario have approximately the same growth rates, then the larger size classes must have settled during late summer to early fall of 1990 which is consistent with Griffiths et al.'s (1991) estimate of first settlement in Lake Ontario. Size classes between 10 and 15 mm may be a result of a settlement event early in the summer of 1991, whereas, the smaller size classes (< 10 mm) are probably a result of a settlement event during mid-summer 1991.

There were variations in size class structure which appear to be associated with location along the Niagara-Toronto region. With increasing distance from Niagara to Hamilton, size of each of the major size classes increased (Figure 36). If growth rates were consistent among these populations, then differences in size of length classes were a result of differences in timing of settlement events, with settlement at between Stoney Creek and Oakville first. If timing of meio-benthos survey, they were too small (< 5 mm) to confidently distinguish between zebra and quagga mussels. The quagga mussels found along the Niagara-Hamilton corridor had average shell lengths that ranged between 11.8 mm (Transect 1) and 22.7 mm (Transect 4). The presence of mussels over 20 mm long at Transect 4 suggest that settlement occurred sometime in 1990 (assuming growth rates of quagga mussels are similar to zebra mussels).

4.5 Summary

Differences in benthic invertebrate community composition were observed between 1981 and 1991. Changes were more obvious in the 5-m benthic communities than in 20-m communities. At 5 m, changes suggestive of improvements in water quality over the period of 1981 to 1991 were generally widespread as indicated by higher taxonomic richness, higher numbers of insects (Ephemeroptera, Chironomidae) and gastropods, and lower numbers of worms (Tubificidae and Naididae). The 20-m communities along the north shore of the lake exhibited changes which also suggested improvements in water quality including higher numbers of lumbriculids, gastropods and sphaeriids. Along the Niagara-Hamilton corridor, the numbers of chironomids at 20 m were lower in 1991 than in 1981 suggesting an effect unrelated to the expected nutrient enrichment scenario. The interpretation of the results are subject to a degree of uncertainty due to subtle differences in methods and timing of surveys between 1981 and 1991.

Depth had the most obvious effects on community structure of those habitat factors examined. In general, 5-m communities were characterized by epibenthic fauna such as gastropods and insects (chironomids, Ephemeroptera, Trichoptera). In contrast, 20-m communities were characterized by infaunal groups such as sphaeriid clams and oligochaete worms.

Low to moderate densities of zebra mussels were found in the western end of Lake Ontario in 1991. Based on size class structure, zebra mussels settled along the shoreline between Stoney Creek and Oakville in the fall of 1990, and between Niagara-on-the-Lake and Beamsville during the spring of 1991. Quagga mussels were found between Niagara-on-the-Lake and Beamsville, and at Oakville. The presence of large quagga mussels at Beamvsville suggested that settlement occurred sometime in 1990.

5.0 LITERATURE CITED

Anderson, A.M. 1990. Selected methods for the monitoring of benthic invertebrates in Alberta Rivers. Environmental Quality Monitoring Branch, Environmental Assessment Division, Alberta Environment, 1990.

Bailey, R.C. 1988. Correlations between species richness and exposures: freshwater molluscs and macrophytes. Hydrobiologia 162:183-191.

Bailey, R.C., and G.L. Mackie. 1986. Reproduction of a fingernail clam in contrasting habitats: life-history tactics? Can. J. Zool. 64:1701-1704.

Barton, D. R. 1986. Nearshore benthic invertebrates of the Ontario waters of Lake Ontario. J. Great Lakes Res. 12:270-280.

Barton, D. R. 1988. Distribution of some common benthic invertebrates in nearshore Lake Erie, with emphasis on depth and type of substratum. J. Great Lakes Res. 14:34-43.

Barton, D. R., and M. Griffiths. 1984. Benthic invertebrates of the nearshore zone of eastern Lake Huron, Georgian Bay, and North Channel. J. Great Lakes Res. 10:407-416.

Barton, D.R., and S.M. Smith. 1984. Insects of extremely small and extremely large aquatic habitats. In, V.H. Resh and D.R Rosenberg (eds), The Ecology of Aquatic Insects. Praeger Publishers, New York. pp 456-483.

Bednarik, A.F., and W.P. McCafferty. 1979. Biosystematic revision of the genus Stenonema (Ephemeroptera: Heptageniidae). Can. Bull. Fish. Aquat. Sci. No. 201. 73 pp.

Bilyj, B., and I. J. Davies. 1989. Description and ecological notes on seven new species of Cladotanytarsus (Chironomidae:Diptera) collected from an experimentally acidified lake. Can. J. Zool. 67:948- 962.

Boesel, M. W. 1985. A brief review of the genus Polypedilum in Ohio, with keys to known stages of species occurring in northeastern United States (Diptera, Chironomidae). Ohio J. Sci. 85: 245 - 262.

Bousfield, E.L. 1958. Fresh-water amphipod crustaceans of glaciated North America. Can. Field Nat. 72:55-113.

Bousfield, E.L. 1989. Revised morphological relationships within the amphipod genera Pontoporeia and Gammaracanthus and the "glacial relict" significance of their postglacial distribution. Can. J. Fish. Aquat. Sci. 46:1714-1725.

Brinkhurst, R.O. 1969. Changes in the benthos of Lake Ontario. Proceedings of the Conference on Changes in Biota of Lakes Erie and Ontario. Bull. Buffalo Soc. Nat. Sci. 25:45-65.

Brinkhurst, R.O. 1986. Guide to the freshwater aquatic microdrile oligochaetes of North America. Can. Spec. Publ. Fish. Aquat. Sci. No. 84. 259 pp.

Brown, H.P. 1976. Aquatic Dryopoid Beetles (Coleoptera) of the United States. Water Pollution Control Research Series 18050 ELD04/72 (2nd Ed.). 82 pp.

Burch, J.B. 1989. North American Freshwater Snails. Malacological Publications, Hamburg, MI. 365 pp.

Cook, D.R. 1974. Water mite genera and subgenera. Mem. Am. Entomol. Inst. No. 21. 860 pp.

Cook, D.G., and M.G. Johnson. 1974. Benthic macroinvertebrates of the St. Lawrence Great Lakes. J. Fish. Res. Bd. Can. 31:763-782.

Crocker, D.W., and D.W. Barr. 1968. Handbook of the crayfishes of Ontario. University of Toronto Press, Toronto. 158 pp.

Culp, J.M., and R.W. Davies. 1980. Reciprocal averaging and polar ordination as techniques for analyzing lotic macroinvertebrate communities. Can. J. Fish. Aquat. Sci. 37:1358-1364.

Dermott, R., J. Mitchell, I. Murray, and E. Fear. 1993. Biomass and production of zebra mussels Dreissena polymorpha) in shallow waters of northeastern Lake Erie. In, T.F. Nalepa and D.W. Schloesser (eds), Zebra Mussels, Biology, Impacts, and Control. CRC Press, Inc., Boca Raton, Florida. pp 390-414.

De Vault, D., P. Bertram, D.M. Whittle, and S. Rang. 1994. Toxic contaminants in the Great Lakes. State of the Lakes Ecosystem Conference. Environment Canada and United States Environmental Protection Agency, EPA 905-D-94-001e.

Doughman, J. S. 1985. Annotated keys to the genera of the tribe Diamesini (Diptera: Chironomidae), descriptions of the female and immatures of Potthastia iberica Tosio, and keys to the known species of Potthastia. Inst. Water Res./Engin. Exp. St.,Univ.Alaska-Fairbanks, Fairbanks, Alaska,Report IWR-107,37 pg.,52 fig..

Epler, J. H. 1987. Revision of the nearctic Dicrotendipes Kieffer, 1913 (Diptera: Chironomidae). Evolutionary Monographs 9,102 pg., 245 fig.

Ferraro, S.P., and F.A. Cole. 1990. Taxonomic level and sample size sufficient for assessing pollution impacts on the southern California Bight macrobenthos. Mar. Ecol. Prog. Ser. 67:251-262.

Ferraro, S.P., and F.A. Cole. 1992. Taxonomic level sufficient for assessing a moderate impact on macrobenthos communities of Puget Sound, Washington, U.S.A. Can. J. Fish. Aquat. Sci. 49:1184-1188.

Furse, M.T., D. Moss, J.F. Wright, and P.D. Armitage. 1984. The influence of seasonal and taxonomic factors on the ordination and classification of running-water sites in Great Britain and on the prediction of their macro-invertebrate communities. Freshwat. Biol. 14:257-280.

Gachter, R., R.A. Vollenweider, and W.A. Glooschenko. 1974. Seasonal variations of temperature and nutrients in the surface waters of Lakes Ontario and Erie. J. Fish. Res. Bd. Can. 31:275-290.

Gray, J.S., M. Aschan, M.R Carr., K.R. Clarke, R.H. Green, T.H. Pearson, R. Rosenberg, and R.M. Warwick. Analysis of community attributes of the benthic macrofauna of Frierfjord/Langesundfjord and in a mesocosm experiment. Mar. Ecol. 46:151-165.

Green, R.H. 1979. Sampling Design and Statistical Methods for Environmental Biologists. John Wiley & Sons, New York. 257 pp.

Green, R.H. 1989. Power analysis and practical strategies for environmental monitoring. Env. Res. 50:195-205.

Griffiths, R.W. 1993. Effects of zebra mussels (Dreissena polymorpha) on benthic fauna of Lake St. Clair. In, T.F. Nalepa and D.W. Schloesser (eds), Zebra Mussels, Biology, Impacts, and Control. CRC Press, Inc., Boca Raton, Florida. pp 415-438.

Griffiths, R.W., D.W. Schloesser, J.H. Leach, and W.P. Kovalak. 1991. Distribution and dispersal of the zebra mussel (Dreissena polymorpha) in the Great Lakes region. Can. J. Fish. Aquat. Sci. 48:1381-1388.

Grodhaus, G. 1987a. Endochironomus Kieffer, Tribelos Townes, Synendotendipes, n. gen. and Endotribelos, n. gen. (Diptera: Chironomidae) of the nearctic region. J. Kansas Ent. Soc. 60: 167-247.

Grodhaus, G. 1987b. Phaenopsectra mortensoni n. sp. and its relationship to other Chironomidae (Diptera) of temporary pools. Ent. Scand. Suppl. 29: 137 - 145.

Haddock, J.D. 1977. The biosystematics of the caddis fly genus Nectopsyche in North America with special emphasis on the aquatic stages. Am. Midl. Nat. 98:382-421.

Hebert, P.D.N., B.W. Muncaster, and G.L. Mackie. 1989. Ecological and genetic studies on

Dreissena polymorpha (Pallas): a new mollusc in the Great Lakes. Can. J. Fish. Aquat. Sc. 46:1587-1591.

Hill, M.O. 1973. Reciprocal averaging: an eigenvector method of ordination. J. Ecol. 61:237-249.

Hill, M.O. 1979. TWINSPAN - A FORTRAN Program for Arranging Multivariate Data in an Ordered Two-way Table by Classification of the Individuals and Attributes. Ecology and Systematics, Cornell University, Ithaca, New York.

Hinch, S.G., and R.C. Bailey. 1988. Within- and among-lake variation in shell morphology of the freshwater clam Elliptio complanata (Bivalvia: Unionidae) from south-central Ontario lakes. Hydrobiol 157:27-32.

Holsinger, J.R. 1976. The freshwater amphipod crustaceans (Gammaridae) of North America. Water Pollution Control Research Series. 18050 ELD04/72 (2nd Ed.). 89 pp.

Integrated Explorations. 1984. A nearshore benthic survey of Lake Ontario. Prepared for the Ontario Ministry of the Environment, Great Lakes Branch. 168 pp.

Integrated Explorations. 1992. Field report on the 1991 Lake Ontario benthos-sediment integration. Prepared for the Ontario Ministry of the Environment, Water Resources Branch. Integrated Explorations Report No. 9105-1, September 1992.

Jackson, G. A. 1977. Nearctic and palaearctic Paracladopelma, Harnisch and Saetheria n. gen. (Diptera: Chironomidae). J. Fish. Res. Bd. Can. 34: 1321 - -1359.

Jackson, D.A. 1993. Multivariate analysis of benthic invertebrate communities: the implications of choosing particular data standardizations, measures of association, and ordination. Hydrobiol. 268:9-26.

Johnson, M.G., and R.O. Brinkhurst. 1971. Associations and species diversity in benthic macroinvertebrates of Bay of Quinte and Lake Ontario. J. Fish. Res. Bd. Can. 28:1683-1697.

Johnson, M.G., and D.H. Matheson. 1968. Macroinvertebrate communities of the sediments of Hamilton Bay and adjacent Lake Ontario. Limnol. Oceanog. 13:99-111.

Kat, P.W. 1982. Effects of population density and substratum type on growth and migration of Elliptio complanata (Bivalvia: Unionidae). Mal. Rev. 15:119-127.

Kilgour, B.W., and G.L. Mackie. 1991. Relationships between demographic features of a pill clam (Pisidium casertanum) and environmental variables. J. N. Am. Benthol. Soc. 10:68-80.

Kinney, W.L. 1972. The macrobenthos of Lake Ontario. Proc. 15th Conf. Great Lakes Res. 1972:53-79. Internat. Assoc. Great Lakes Res.

Klemm, D.J. 1985. A guide to the freshwater Annelida (Polychaeta, Naidid and Tubificid Olilgochaeta, and Hirudinea) of North America. Kendall/Hunt Publ. Dubuque, Iowa. 198 pp.

Krieger, K.A. 1984. Benthic macroinvertebrates as indicators of environmental degradation in the southern nearshore zone of the central basin of lake Erie. J. Great Lakes Res. 10:197-209.

Krieger, K.A. 1985. Snail distributions in Lake Erie: the influence of anoxia in the southern central basin nearshore zone. Ohio J. Sci. 85:230-244.

Legendre, P., and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio 80:107-138.

Lewis, P.A. 1974. Taxonomy and ecology of Stenonema mayflies (Heptageniidae: Ephemeroptera). Environ. Monit. Ser. EPA-640/4-74-006. 81 pp.

MacIsaac, H.J., W.G. Sprules, and J.H. Leach. 1991. Ingestion of small-bodied zooplankton by zebra mussels (Dreissena polymorpha): can cannibalism on larvae influence population dynamics? Can. J. Fish. Aquat. Sci. 48:2051-2060.

Mackie, G.L. 1991. Biology of the exotic zebra mussel, Dreissena polymorpha, in relation to native bivalves and its potential impact in Lake St. Clair. In M. Munawar and T. Edsall (eds), Environmental Assessment and Habitat Evaluation of the Upper Great Lakes Connecting Channels, Hydrobiol. 219:251-268.

Mackie, G.L. 1992. Biology of the Corbiculacean Clams of North America. Manuscript.

Mackie, G.L. 1993. Biology of the zebra mussel (Dreissena polymorpha) and observations of mussel colonization on unionid bivalves in Lake St. Clair of the Great Lakes. In, T.F. Nalepa and D.W. Schloesser (eds), Zebra Mussels, Biology, Impacts, and Control. Lewis Publishers. pp 143-152.

Mackie, G.L., and S.U. Qadri. 1973. Abundance and diversity of mollusca in an industrialized portion of the Ottawa River near Ottawa-Hull, Canada. J. Fish. Res. Bd. Can. 30:167-172.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. 27:209-220.

May, B., and J.E. Marsden. 1992. Genetic identification and implications of another invasive pest of dreissenid mussel in the Great Lakes. Can. J. Fish. Aquat. Sci. 49:1501-1506.

McBride, G.B., J.C. Loftis, N.C. Adkins. 1993. What do significance tests really tell us about the environment? Env. Mgmt. 17:423-432.

Merritt, R.W., and K.W. Cummins. 1984. An Introduction to the Aquatic Insects of North America, 2nd Edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Metcalfe, J.L. 1989. Biological water quality assessment of running waters based on macroinvertebrate communities: history and present status in Europe. Environ. Poll. 60:101-139.

Minns, C.K., G.E. Owen, and M.G. Johnson. 1986. Nutrient loads and budgets in the Bay of Quinte, Lake Ontario, 1965-81, p.59-76. In C.K. Minns, D.A. Hurley, and K.H. Nicholls (eds) Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. Can. Spec. Publ. Fish. Aquat. Sci. 86:270 pp.

Nalepa, T.F. 1991. Status and trends of the Lake Ontario macrobenthos. Can. J. Fish. Aquat. Sci. 48:1558-1567.

Neilson, M., S. L'Italien, V. Glumac, D. Williams, and P. Bertram. 1994. Nutrients: trends and system response. State of the Lakes Ecosystem Conference. Environment Canada and United States Environmental Protection Agency, EPA 905-D-94-001d.

Oliver, D. R., and M. E. Roussel. 1983. The insects and arachnids of Canada. Part 11. The genera of larval midges of Canada, Diptera: Chironomidae. Research Branch, Agriculture Canada Publ. 1746, 263 pg.

Ontario Ministry of Natural Resources (OMNR). 1985. Guide to Taxonomic Standards for the Identification of Ontario Freshwater Invertebrates. Draft Report, 1985.

Pathy, D.A., and G.L. Mackie. 1992. Life history and demographics of populations of the zebra mussel (Dreissena polymorpha) in Lake St. Clair and Lake Erie. In, G.L. Mackie, D. Pathy, P. Gillis and E. Dobson, Biology and Impact of Zebra Mussels in Lake St. Clair and Lake Erie. A Final Report for Project 443G to the Ontario Ministry of Environment.

Pennak, R.W. 1989. Fresh-water Invertebrates of the United States. Third edition. North America. Wiley Interscience Publications, New York. 628 pp.

Peterman, R.M. 1990. Statistical power analysis can improve fisheries research and management. Can. J. Fish. Aquat. Sci. 47:2-15.

Pielou, E.C. 1975. Ecological Diversity. Wiley, New York. 165 pp.

Plafkin, J.L., M.T. Barbour, K.D. Porter, S.K. Gross, and R.M. Hughes. 1989. Rapid bioassessment protocols for use in streams and rivers: benthic macroinvertebrates and fish. United States Environmental Protection Agency, Office of Water. EPA/440/4-89/001

Poddubnaya, T.L. 1980. Life cycles of mass species of Tubificidae (Oligochaeta). In, R.O. Brinkhurst and D.G. Cook (eds), Aquatic Oligochaete Biology. Plenum Press, New York. pp 175-184.

Reckhow, K.H. 1994. Importance of scientific uncertainty in decision making. Env. Mgmt. 18:161-166.

Reed, C. 1978. Species diversity in aquatic micro-ecosystems. Ecology 59:481-488.

Roback, S. S. 1957. The immature Tendipedidae of the Philadelphia area (Diptera: Tendipedidae). Monogr. Acad. Nat. Sci. Phila. 9, 152 pg.

Roback, S. S. 1963. The genus Xenochironomus (Diptera: Tendipedidae) Kieffer,taxonomy and immature stages. Trans. Am. Entomol. Soc. 88: 235 - 245.

Roback, S. S. 1985. The immature chironomids of the eastern United States VI. Pentaneurini - Genus Ablabesmyia. Proc. Acad. Nat. Sci. Phila. 137: 153- 212.

Rohlf, F.J. 1993. NTSYS-pc: Numerical Taxonomy and Multivariate Analysis System, Version 1.80. Exeter Software, Setauket, NY.

Ross, H.H. 1944. The caddis flies, or Trichoptera of Illinois. Bull. Ill. Nat. Hist. Sur. 23. 326 pp.

Saether, O. A. 1969. Some nearctic Podonominae, Diamesinae, and Orhtocladiinae (Diptera: Chironomidae). Bull. Fish. Res. Bd. Can. No. 170, 154 pg.

Saether, O. A. 1973. Taxonomy and ecology of three new species of Monodiamesa Kieffer, with keys to nearctic and palaearctic species of the genus (Diptera: Chironomidae). J. Fish. Res. Bd. Can. 30: 665 - 679.

Saether, O. A. 1975. Nearctic and palaearctic Heterotrissocladius (Diptera: Chironomidae). Bull. Fish. Res. Bd. Can. No. 193, 67 pg.

Saether, O. A. 1977. Taxonomic studies on Chironomidae: *Nanocladius*, *Pseudochironomus*, and the *Harnischia* complex. Bull. Fish. Res. Bd. Can. No. 196, 143 pg.

Seed, R. 1980. Shell growth and form in the Bivalvia. In, D.C. Rhoads and R.A. Lutz (eds), Skeletal Growth of Aquatic Organisms. pp 23-67.

Servos, M.R., J.B. Rooke, and G.L. Mackie. 1985. Reproduction of selected mollusca in some low alkalinity lakes in south-central Ontario. Can. J. Zool. 63:511-515.

Shannon, C.E., and W. Weaver. 1949. The Mathematical Theory of Communication. The University of Illinois Press, Urbana, IL. 117 pp.

Simpson, K. W., and R. W. Bode. 1980. Common larvae of Chironomidae (Diptera) from New York state streams and rivers with particular reference to the fauna of artificial substrates. New York State Museum Bull no. 439, 105 pg.

Simpson, K. W., R. W. Bode and P. Albu. 1983. Keys for the genus *Cricotopus* adapted from "Revision der Gattung *Cricotopus* van der Wulp und ihrer Verwandten (Diptera, Chironomidae)" by M. Hirvenoja. New York State Museum Bull No. 450, 133 pg.

Taylor, L.R. 1961. Aggregation, variance and the mean. Nature (Lond.) 189:723-735.

Thorp, J.H., A.P. Covich. 1991. Ecology and Classification of North American Freshwater Invertebrates. Academic Press Inc, San Diego. 911 pp.

Townes, H. K. 1945. The nearctic species of Tendipedidae (Chironomidae). Am. Midl. Nat. 34: 1 - 206.

Warwick, R.M. 1988a. Analysis of community attributes of the macrobenthos of Frierfjord/Langesundfjiord at taxonomic levels higher than species. Mar. Ecol. Prog. Ser. 46:167-170.

Warwick, R.M. 1988b. The level of taxonomic discrimination required to detect pollution effects on marine benthic communities. Mar. Poll. Bull. 19:259-268.

Warwick, R.M., M.R. Carr, K.R. Clarke, J.M. Gee, and R.H. Green. 1988. A mesocosm experiment on the effects of hydrocarbon and copper pollution on a sublittoral soft-sediment meiobenthic community. Mar. Ecol. 46:181-191.

Warwick, R.M., H.M Platt, K.R. Clarke, J. Agard, J. Gobin. 1990. Analysis of macrobenthic and meiobenthic community structure in relation to pollution and disturbance in Hamilton Harbour, Bermuda. J. Exp. Mar. Biol. Ecol. 138:119-142.

Washington, H.G. 1984. Diversity, biotic and similarity indices: a review with special relevance to aquatic ecosystems. Water Res. 18:653-694.

Wiederholm, T. 1983. Chironomidae of the holarctic region. Keys and diagnoses. Part 1. Larvae. Ent.Scand. Suppl. No. 19,457 pg.

Wiederholm, T. 1986. Chironomidae of the holarctic region. Keys and diagnoses. Part 2. Pupae. Ent. Scan. Suppl. No. 28, 482 pg.

Wiggins, G.B. 1977. Larvae of the North American caddisfly genera (Trichoptera). University of Toronto Press, Toronto. 401 pp.

Wilkinson, L. 1990. SYSTAT: The System for Statistics. Evanston, IL.

Williams, W.D. 1976. Freshwater Isopods (Asellidae) of North America. Water Pollution Control Research Series 18050 ELD05/72 (2nd Ed.). 45 pp.

Winnel, M. H., and D. J. Jude. 1984. Associations among chironomidae and sandy substrates in nearshore Lake Michigan. Can. J. Fish. Aq. Sci. 41:174-179.

Yamamoto, T., and G.B. Wiggins. 1964. A comparative study of the North American species of the caddisfly genus Mystacides (Trichoptera: Leptoceridae). Can. J. Zool. 42:1105-1126.

Zar, J.H. 1984. Biostatistical Analysis, 2nd Edition. Prentice Hall, New Jersey, NY. 718 pp.

Table 1. List of taxonomic keys, taxonomists, and external authorities used to identify certain taxonomic groups.

Taxon	Initial Taxonomist	External Authority	References
Oligochaeta	Ms W. Cook Mr. W.B. Morton	Dr. D.R. Barton Department of Biology University of Waterloo 200 University Ave. W. Waterloo, Ontario N2L 3G1	1
Hirudinea	Mr. W.B. Morton		2
Amphipoda	Mr. W.B. Morton		3,4,5
Isopoda	Mr. W.B. Morton		6
Decapoda	Mr. W.B. Morton		7
Chironomidae	Mr. W.B. Morton	Dr. L. Ferrington University of Kansas 2291 Irving Hill Drive Raymond Nichols Building Lawrence, Kansas 66045	8-27
Ephemeroptera	Mr. W.B. Morton		28,29
Trichoptera	Mr. W.B. Morton	Mr. M.A. Floyd & Dr. J. Morse Department of Entomology, Clemson University, Clemson, SC 29634	30-33
Coleoptera	Mr. W.B. Morton		34
Acari	Mr. W.B. Morton	Dr. I. Smith	35
Gastropoda	Dr. G.L. Mackie		36
Bivalvia	Dr. G.L. Mackie		37-38
General	W.B. Morton		39-41

1 Brinkhurst (1986)
2 Klemm (1985)
3 Bousfield (1958)
4 Bousfield (1989)
5 Holsinger (1976)
6 Williams (1976)
7 Crocker and Barr (1968)
8 Bilyj and Davies (1989)
9 Boesel (1985)
10 Doughman (1985)
11 Epler (1987)
12 Grodhaus (1987a)
13 Grodhaus (1987b)
14 Jackson (1977)
15 Oliver and Roussel (1983)
16 Roback (1957)
17 Roback (1963)
18 Roback (1985)
19 Saether (1969)
20 Saether (1973)
21 Saether (1975)
22 Saether (1977)
23 Simpson and Bode (1980)
24 Simpson et al. (1983)
25 Townes (1945)
26 Wiederholme (1983)
27 Wiederholme (1986)
28 Bednarik and McCafferty (1976)
29 Lewis (1974)
30 Haddock (1977)
31 Ross (1944)
32 Wiggins (1977)
33 Yamamoto and Wiggins (1964)
34 Brown (1976)
35 Cooke (1987)
36 Burch (1989)
37 May and Marsden (1992)
38 Mackie (1992)
39 Merrit and Cummins (1984)
40 Pennak (1989)
41 Thorp and Covich (1991)

Table 2. Taxonomic inconsistencies between the 1981 and 1991 data sets.

1981 Taxon	Problem	Solution
Annelida. Oligochaeta		
Chaetogaster cristallinus	*C. cristallinus* is a synonym with *C diaphanus* (Brinkhurst, 1986)	1981 data changed to *C diaphanus*
Stylaria fossularia	*S. fossularia* is a synonym of *S. lacustris* (Brinkhurst, 1986)	1981 data changed to *S. lacustris*
Limnodrilus newaensis	not an appropriate name (Brinkhurst, 1986)	1981 data changed to *Tubifex nerthus*
Crustacea.		
Pontoporeia hoyi	old name (Bousfield, 1989)	1981 data changed to *Diaporeia* sp.
Asellus (all)	old name (Pennak, 1989; Thorp and Covich, 1991)	1981 data changed to *Caecidotea* sp
Diptera: Chironomidae		
Microtendipes pedellus	No species keys available. Identified only to genus in 1991.	1981 not changed
Parachironomus sp.	Separated into species in 1991.	1981 data not changed
Paralauterborniella	Keys to species used in 1991 to identify these to *P. nigrohalteralis*	1981 data not changed
Paratendipes sp.	Keys to species used in 1991 to identify these to *P. albimanus*	1981 data not changed
Phaenopsectra sp.	1981 specimens likely included both *P. obediens* and *Tribelos jucundum*	1981 data not changed
Ablabesmyia sp.	1981 specimens likely included both *A. mollochi* and *A. monilis*	1981 data not changed
Oecetis avara	1991 specimens not identified to species, except one male pupa	1981 data not changed
Mollusca:		
Gyraulus parvus	1981 specimens may have included some *G. deflectus*	1981 data not changed
Helisoma anceps	1981 specimens may have included some *Pierosoma trivolvis*	1981 data not changed
Stagnicola emarginata	1981 specimens may have included some *Fossaria obrussa*	1981 data not changed

Table 3. Analysis of variance design used to evaluate variation in response variables due to Transect (1-25), Depth (5m, 20m), and Year (1981, 1991) effects, as well as possible interactions. Note that Year and Depth are considered "fixed effects", while Transect is considered a "random effect".

Source	df	MS	F-test
Year	y-1 = 1	MS(Y)	MS(Y)/MS(Y·T)
Depth	d-1 = 1	MS(D)	MS(D)/MS(D·T)
Transect	t-1 = 24	MS(T)	MS(T)/MS(Error)
Year·Depth	(y-1)(d-1) = 1	MS(Y·D)	MS(Y·D)/MS(Y·D·T)
Year·Transect	(y-1)(t-1) = 24	MS(Y·T)	MS(Y·T)/MS(Error)
Depth·Transect	(d-1)(t-1) = 24	MS(D·T)	MS(D·T)/MS(Error)
Year·Depth·Transect	(y-1)(d-1)(t-1) = 24	MS(Y·D·T)	MS(Y·D·T)/MS(Error)
Error	ydt(n-1) = 200	MS(Error)	
Total	ydtn-1 = 299		

Table 4. Significance of analyses of variance effects with various response variables, including both taxonomic densities and community descriptors. Results are for untransformed data. Log_e and $X^{0.25}$ transformed data resulted in slightly more conservative tests but the same conclusions. The estimates under R^2 indicate the percentage of variation accounted for in the model.

Response Variable	YEAR (Y)	DEPTH (D)	TRANSECT (T)	Y•D	Y•T	D•T	Y•D•T	R^2
i. Summary Indices								
Richness	0.0015	0.0002	0.0001	0.0041	0.0001	0.0001	0.0001	0.834
Shannon's Diversity	0.0001	0.0277	0.0001	0.6889	0.0001	0.0001	0.0001	0.779
Total Invertebrates	0.3310	0.0627	0.0001	0.8118	0.0001	0.0001	0.0001	0.768
ii. Individual Taxa								
Lumbriculidae	0.1450	0.0057	0.0001	0.3317	0.0001	0.0001	0.0001	0.808
Naididae	0.0128	0.1568	0.0001	0.1739	0.0001	0.0001	0.0001	0.806
Tubificidae	0.0334	0.6216	0.0001	0.4069	0.0001	0.0001	0.0001	0.670
Enchytraeidae	0.7745	0.7211	0.0001	0.2221	0.0001	0.0001	0.0001	0.785
Polychaeta	0.3672	0.6064	0.0001	0.7998	0.0001	0.0001	0.0001	0.745
Nemertea	0.1924	0.0524	0.0001	0.4290	0.0001	0.0001	0.0001	0.736
Amphipoda	0.2397	0.2159	0.0001	0.0188	0.0001	0.0001	0.0001	0.909
Isopoda	0.6963	0.1612	0.0001	0.2085	0.0001	0.0029	0.0137	0.582
Ephemeroptera	0.2102	0.2180	0.0001	0.1955	0.0001	0.0001	0.0001	0.845
Trichoptera	0.4724	0.0188	0.0001	0.6111	0.0003	0.0001	0.0002	0.656
Tanypodinae	0.7244	0.2996	0.0017	0.0270	0.601	0.0012	0.0003	0.557
Diamesinae	0.9912	0.0187	0.0479	0.2837	0.0100	0.1477	0.1655	0.440
Orthocladiinae	0.3204	0.0919	0.0001	0.9104	0.0001	0.0001	0.0001	0.799
Chironomini	0.2048	0.0633	0.0001	0.1209	0.0001	0.0001	0.0001	0.807
Tanytarsini	0.2084	0.2838	0.0001	0.0419	0.0001	0.0001	0.0001	0.812
Gastropoda	0.0348	0.0035	0.0001	0.0408	0.0001	0.0001	0.0001	0.828
Sphaeriidae	0.1514	0.0282	0.0001	0.4355	0.0001	0.0001	0.0001	0.832

Table 5. Analysis of variance table testing for differences in the change of Correspondence Analysis (CA) axis scores from 1981 to 1991 (Year effect) in mussel infested and uninfested locations (Infest effect).

CA axis	Source	df	MS	SS	F	P
1	Infest	1	0.055	0.055	0.149	0.701
	Year	1	6.890	0.890	18.531	0.000
	Infest·Year	1	0.029	0.029	0.078	0.781
	Error	46	17.10	0.372		
2	Infest	1	0.002	0.002	0.007	0.933
	Year	1	1.159	1.159	5.382	0.025
	Infest·Year	1	0.004	0.004	0.018	0.894
	Error	46	9.907	0.215		
3	Infest	1	0.676	0.676	2.102	0.154
	Year	1	0.050	0.050	0.156	0.695
	Infest·Year	1	0.738	0.738	2.295	0.137
	Error	46	14.78	0.321		

Table 6. Major sediment characteristics at each of the stations in 1981 and 1991.

Tran	5 m			20 m		
	1981	1991	change	1981	1991	change
1	bedrock	bedrock		silt	silt	
2	bedrock	bedrock/gravel		gravel	clay	finer
3	bedrock	bedrock		bedrock/sand	silt	finer
4	bedrock	bedrock		bedrock	sand	finer
5	bedrock	cobble		silt	clay	
6	silt	sand	coarser	silt	sand	
7	bedrock	bedrock		bedrock	bedrock	
8	bedrock	clay	finer	clay	bedrock	coarser
9	bedrock	bedrock		bedrock	bedrock	
10	bedrock	clay	finer	silt	clay	
11	sand	sand		silt	clay	
12	clay	cobble	coarser	gravel/ sand	gravel/ sand	
13	sand	sand		bedrock	cobble	finer
14	bedrock	bedrock	finer	bedrock	bedrock	
15	bedrock	bedrock		bedrock/gravel	sand	finer
16	sand	cobble	coarser	gravel	sand	finer
17	bedrock	bedrock		bedrock	bedrock	
18	bedrock	bedrock		sand	bedrock	coarser
19	bedrock	bedrock		sand	clay	finer
20	bedrock	bedrock		sand	sand	
21	sand	sand		sand	sand	
22	bedrock	bedrock		silt	bedrock	coarser
23	gravel	bedrock	coarser	silt	silt	
24	gravel	gravel		silt	silt	
25	bedrock	cobble	finer	silt	sand	

Table 7. Percent cover of Cladophora at each of the stations in 1981 and 1991, at 5 m. Data are not presented for the 20 m depths because Cladophora was present at 20 m at only one station (Transect 17, 1991)

Transect	1981	1991
1	80	75
2		50
3		95
4		90
5		40
6		
7	100	
8	100	50
9	80	50
10	30	
11		
12		
13		
14	50	30
15	100	
16	50	90
17	100	50
18	1	50
19	100	
20	100	20
21	5	
22	100	
23	20	
24		
25		

Table 8. Results from ANOVAs testing for differences in mean ordination (Correspondence Analysis) axis scores between Years (1981 and 1991) for at 5 and 20 m.

CA axis	difference	t	df	p
5 m				
1	0.817	-3.905	24	0.006
2	-0.159	1.400	24	0.204
3	-0.027	0.130	24	0.900
20 m				
1	0.066	-0.049	23	0.679
2	-0.767	5.052	23	<0.000
3	0.696	-5.335	23	<0.000

Table 9. Summary of taxa contributing to structure of Correspondence Analysis axes describing community structure of benthos from 5 and 20 m at 25 transects along the Canadian side of Lake Ontario. The summary is based on information in Appendix E.

Axis	Taxon	Contribution to Axis	Squared Correlation with Axis
1	Tubificidae	0.266	0.482
	Amphipoda	0.215	0.453
	Gastropoda	0.237	0.436
	Naididae	0.165	0.317
2	Chironomini	0.143	0.375
	Naididae	0.212	0.303
	Lumbriculidae	0.227	0.340
3	Gastropoda	0.326	0.361
	Chironomini	0.166	0.349
	Tanytarsini	0.137	0.374

Table 10: TWINSPAN-ordered table of samples and species for the 1981 and 1991 data based on the ranked relative abundance of taxonomic summary groups. Results for replicate samples (n=3) have been averaged.

Year 1981	88888	-8------------8--8-8	888-------8-8-88-8-8	888888888888888888	88-8--88--88-8-8--	8888	--------8--	---
1991	-----	9-999999999999-99-9-	---9999999-9-9--9-9-	------------------	--9-99--99--9-9-99	----	99999999-99	999
Depth 20m	-----	--------------------	-2-----2-2-222-22--2	2-2-2-2---2-2-22-2	22-222-222-22222-2	2222	22222-22222	222
5m	55555	55555555555555555555	5-55555-5-5---5--55-	-5-5-5-555-5-5--5-	--5---5---5-----5-	----	-----5----2	---
Ephemeroptera	-----	-----1---21-1--1--1-	--------------------	----1-------------	------------------	----	----1------	---
Trichoptera	-3-32	-31-113-1-1111313221	--11-----111-11---11	---1-1-----111--3-	--1-------1-11----	----	-----------	---
Gastropoda	43325	44356445314366556636	-2132--11--1321-1141	2-12113----1-----1	--5-211--33-131-23	--1-	43212--3123	---
Dreissenidae	-----	2-52121----1------1-	---1----------------	------------------	--1---------------	----	11----1----	---
Nemertea	-----	-----------1-----1--	------------------1-	--111---2111------	1-----------------	----	-----1-11--	---
Chironomini	-1132	--211132333221321142	3134545353331152333-	111111121111222131	1-1-1-1-111111-1--	111-	--1--211-11	-11
Diamesinae	---1-	----1-112111--------	1111--111-11-11-111-	-2---1-------1----	-1-----1----------	----	---------11	-11
Tanytarsini	-2-22	-1211111353312131-3-	34122213431553353134	21----1-11-1112211	31-111---311-111--	1-11	-----3-1111	222
Orthocladiinae	-1242	142-1222333321321--1	1313-33522331251412-	212311--2212---12-	1--1121-111-------	11--	-1--1111-11	134
Tanypodinae	-2112	1-11122-121222-2112-	1113-1-2221-111-1-11	1122111----11111--	221211-1-21123-2--	---1	-------1-1-	2-1
Enchytraedae	-----	--------------1-1-21	-1------------1--1--	--------1--1--11--	-----------1------	-2--	-----------	---
Naididae	56656	33344432333132312113	65353365356455325515	666656666666666666	33132143-334332-13	1334	-1113123421	--2
Isopoda	--2--	----131221111-321332	-2-1----33---21-----	2-11-11----111---2	12-111112312333231	3---	-------1---	1-1
Amphipoda	53333	65353453445645251245	331121--3213-13531-1	1222-2-211-2-3-111	344411223212245365	5665	-21-21-145-	331
Sphaeriidae	-12--	13123321211311413332	33212--41-1345-22453	2111224---4---5214	433343113333243333	3133	64654455545	516
Polychaeta	-2---	---1-----------1----	-1------------------	------------------	--1---1--1-------2	----	-----------	---
Lumbriculidae	--1--	1--121111-121-11111-	-3-1---113-122121-1-	--1-11----1-1-1111	1213-1--311------3	3434	35355-33434	563
Tubificidae	111--	135233153121111-213-	4361663-354423344535	233165321333353342	664666666566645655	4133	24555655335	411

Sample Group	GR1	GR2	GR3	GR4	GR5	GR6	GR7	GR8
Number of Taxa	20.2	44.0	31.3	25.2	25.9	15.8	22.5	20.6
Shannon Diversity	2.9	3.6	3.5	2.3	3.1	2.3	3.0	2.3
Total Individuals	7490	45112	31387	51210	50477	39936	21841	11043
Number of Samples								
Rock	5	17	9	11	6	0	1	1
Gravel/Sand	0	2	8	3	3	3	6	1
Silt/Clay	0	1	3	4	9	1	4	1
Summary Groups (#/m2)								
Ephemeroptera	0	269	0	2	0	0	4	0
Trichoptera	314	675	64	172	60	0	0	0
Isopoda	93	726	442	219	816	722	1	44
Hydrozoa	0	389	263	0	1024	0	22	13
Nemertea	0	11	21	144	7	0	16	0
Amphipoda	866	12520	1160	1194	4100	18254	1888	887
Chironomini	161	2083	2259	559	178	53	190	72
Diamesinae	8	75	93	85	5	0	15	33
Tanytarsini	153	4543	2856	250	293	69	300	343
Orthocladiin	586	1957	1686	870	56	74	111	715
Tanypodinae	119	665	361	361	402	16	52	91
Gastropoda	866	11338	670	285	1128	11	683	0
Dreissenidae	0	358	3	0	6	0	22	0
Sphaeriidae	102	1581	3637	1529	2503	3577	6309	2057
Polychaeta	42	38	6	0	28	0	0	0
Enchytraedae	0	71	13	17	9	244	0	0
Lumbriculidae	8	354	454	125	381	6316	4880	5582
Naididae	4102	3659	7843	32613	3924	5090	563	60
Tubificidae	68	1308	8113	12726	23589	5510	6667	1086
Chironomidae	1028	9323	7256	2126	934	212	669	1254
Oligochaeta	4178	5408	16425	45482	27903	17160	12114	6728

Note: The abundance rankings of taxa in samples were based on percent contribution of sample total and are as follows:
0, not present; 1, 0-2%; 2, >2-5%; 3, >5-15%, 4, >15-25%; 5, >25-50%; 6, >50-100%.
Rock substrata includes bedrock, boulders and cobble. Richness was calculated based on the composite number of taxa found at sites. Diversity was calculated using mean station results.

Table 11. Mantel's correlation matrix of community structure with physical variables. Analysis included total variation (all transects, depths, years), and reduced matrices for each year and depth combination. *P*-values for the correlations are given in brackets below the correlation.

	Depth	Fetch	Upwelling	Location	*Cladophora*	Substrate
Total Variation (n=100)	**0.093** **(<0.01)**	**0.109** **(<0.01)**	0.050 (0.18)	**0.099** **(0.02)**		-0.036 (0.29)
1981, 5m (n=25)		0.069 (0.20)	**0.622** **(<0.01)**	**0.397** **(<0.01)**	-0.113 (0.06)	-0.109 (0.30)
1981, 20m (n=24)		0.119 (0.09)	0.166 (0.14)	-0.125 (0.07)		**0.255** **(<0.01)**
1991, 5m (n=25)		**0.235** **(0.02)**	-0.047 (0.47)	0.146 (0.08)	-0.048 (0.38)	0.101 (0.19)
1991, 20m (n=25)		**0.137** **(0.02)**	**0.274** **(0.02)**	**0.193** (<0.02)		-0.007 (0.49)

Table 12. Results from ANOVAs testing for differences in mean ordination (Correspondence Analysis) axis scores among substrate classes at 5 and 20 m and in 1981 and 1991.

CA axis	Source	df	SS	MS	F	P
1981, 5 m						
1	substrate	4	3.472	0.868	2.255	0.099
	error	20	7.699	0.385		
2	substrate	4	1.543	0.386	1.908	0.149
	error	20	4.044	0.202		
3	substrate	4	0.946	0.237	1.226	0.332
	error	20	3.861	0.193		
1981, 20 m						
1	substrate	4	0.477	0.119	0.380	0.820
	error	19	5.963	0.314		
2	substrate	4	0.960	0.240	0.680	0.615
	error	19	6.710	0.353		
3	substrate	4	0.409	0.102	0.751	0.570
	error	19	2.588	0.136		

Table 12. continued

CA axis	Source	df	SS	MS	F	P
1991, 5 m						
1	substrate	4	0.417	0.104	0.306	0.870
	error	20	6.800	0.340		
2	substrate	4	0.697	0.174	0.923	0.470
	error	20	3.780	0.189		
3	substrate	4	3.771	0.943	2.557	0.069
	error	20	7.316	0.366		
1991, 20 m						
1	substrate	4	1.432	0.358	3.500	0.025
	error	20	2.045	0.102		
2	substrate	4	2.624	0.656	1.384	0.275
	error	20	9.479	0.474		
3	substrate	4	1.448	0.362	2.113	0.117
	error	20	3.426	0.171		

Table 13. TWINSPAN-ordered table of samples and species for the 1991 data based on the ranked relative abundance of individual taxa. Results for replicate samples (n=3) have been averaged. Taxa occuring in less than 7 of the 150 replicate samples were excluded from the analysis

Depth	555555	5555555	5555555	22222 00000	2222222222222 0000000000000	55555	2222222 0000000
Transect	123457	1122222 8902345	11112 8945671	11111 23457	12222 22111 7101458923649	1111 60123	1 1234560
Oecetis	----1-	111112-	1------	-----	-------------	-----	-------
Hydrozetes	--1-1-	-11-1--	-----1-	-----	-------------	-----	-------
Dugesia tigrina	------	122-231	-----2-	-----	----------1--	-----	-------
Orconetes propinquus	--111-	---1-1-	-----1-	-----	-------------	-----	-------
Pseudochironomus	------	111111-	------1	-----	--1----------	-----	-------
Amnicola limosa	-13453	1112231	-111-21	-----	----------11-	-----	----1--
Bythinia tentaculata	1111--	---111-	-------	-----	-------------	-----	1------
Pleurocera acuta	3132-2	11-11--	1-1--2-	----1	-------------	-----	-1-----
Pisidium fallax	--11-1	----11-	------1	-----	-------------	-----	-------
Caenis	-----1	---1-1-	----21-	-----	-------------	-----	----1--
Mystacides	---111	1--13--	111----	-----	-------------	-----	-------
Torrenticola	----1-	-11--1-	--1-11-	-----	-------------	-----	-------
Cura foremanii	1-3311	-21----	111-11-	1----	-------------	-1---	-------
Crangonyx	-----1	-----21	-1---1-	-----	-----------1-	-----	-------
Pseudosmittia	----11	21111--	1-21-1-	-----	--------1----	-----	-------
Chaetogaster diaphanus	-----1	-11----	1---11-	-----	-------------	-----	-------
Fossaria obrussa	---111	-1111-1	-------	----1	-------------	-----	--1----
Probythinella lacustris	-113--	33555--	-----2-	-----	------------1	-----	311----
Stagnicola catascopium	-1----	-112-1-	-------	-----	--------2----	-----	-------
Dreissena polymorpha	352112	11---1-	11-----	-----	1------------	-----	11-----
Nais pseudobtusa	-1----	-11-1--	-------	-----	-----------1-	-----	-------
Porohmannella	----1-	-11-11-	-----1-	----1	--------1----	-----	-------
Gammarus fasciatus	635433	6335135	1-3332-	1---1	111-131-1-2-1	-3-1-	-21-2-1
Caecidotea racovitzae	------	-1-1--1	-----1-	-----	-------------	-1---	-------
Paratendipes albimanus	--1-1-	----11-	------1	-----	------------1	-----	-----1-
Cladotanytarsus	------	111--3-	------1	---11	----------1--	-----	-------
Gyraulus parvus	1-11-1	-------	-------	-----	-------------	-----	31-----
Physella gyrina	323121	1343211	111-121	-----	1-11--11--111	-----	-1-----
Hydroptila	-1--1-	11-1---	1-1----	---11	-------------	-----	-------
Gyraulus deflectus	-11-21	-12----	11--11-	----1	-------1-----	-----	-------
Helisoma anceps	1-1111	--11-11	33----1	-1---	--1-121------	-11--	-------
Valvata tricarinata	--3331	1111311	213--13	-----	--11--1--11--	--1--	11112--
Pisidium nitidum	--11--	1---11-	--1--11	--1-1	--1----1-----	-----	-------
Hyalella azteca	--1-24	-343131	134335-	1-12-	--2----11-1-2	112--	----1--
Helobdella stagnalis	-----1	----111	1-2-1--	-----	--11------1--	-----	-------
Dicrotendipes fumidus	----11	1111---	33-1111	-1---	1------------	-1---	-------
Microtendipes	------	21111--	--2132-	--111	--1-------111	-----	-------
Cricotopus curtus	11--1-	-------	112132-	--1--	-------------	11-1-	-1-----
Psectrocladius simulans	12----	1-11---	21--111	-----	------1------	11-1-	-------
Conchapelopia	-1---2	11211--	3111211	-1-1-	--1----------	---1-	-------
Phaenopsectra obediens	------	-----1-	-1-4-1-	-----	----------1--	----2	-------
Stictochironomus	----1-	-----1-	--3-113	-----	---1----11-1-	-----	-------
Potthastia longimana	----1-	-------	1121111	1----	--1----------	-1--1	-------
Paratanytarsus ?	------	1------	113343-	111--	-------------	-----	-------
Sphaerium striatinum	1-1111	-----1-	------1	-----	---1----111--	-----	1------
Stylaria lacustris	334134	11211--	332132-	-4121	3----------3-	-111-	-11-21-
Lebertia	--1-11	---1111	21----1	-----	---1--112----	-1-11	-------
Limnesia	------	-1-12-1	--1---2	-----	--11-1---1---	---21	-------
Prostoma graecense	------	----1--	-----11	-----	1------------	1----	-------
Procotyla fluviatilis	------	----11-	1------	-----	1-1----------	-----	-------
Tanytarsus	-31-11	211213-	1113433	-1111	1--11--12-3-2	31221	-------
Ablabesmyia monilis	-1--1-	11-11--	---1-1-	-2111	-------------	-----	-------
Nais communis	-1--1-	1---1--	---1---	-1---	--------1----	-1-1-	-------
Nais variabilis	-1--11	111-11-	1131-1-	-1---	--------1--1-	-123-	-------
Aturus	----1-	-------	-11----	--111	-------------	-----	-------
Hygrobates	11112-	1-1-122	1212111	--122	1-11-2-13-111	-1-1-	-------
Caecidotea	----13	11-2123	112311-	--122	12--311133-2-	-2---	------1
Dicrotendipes	------	1----1-	111-1--	-111-	--1----------	---11	-------
Cricotopus	------	1------	11----1	-11-1	-------------	-1-1-	-------
Psectrocladius?	------	-------	11-1--2	----1	---1---------	---22	-------
Unionicola	------	-1-1111	-1-----	1---1	1---1---1---1	-----	-------
Hydridae	------	-11-11-	-------	---4-	--1----------	-----	-------
Hydrolimax grisea	--2--1	11--234	--1----	--122	1-1--21-311-1	-1---	-------
Stempellina bausei	------	-------	----111	----1	----------3--	-----	-------
Zavrelia	------	1-12---	-------	-2-12	--1-------2--	-----	-------
Procladius	11111-	11-----	11-----	---11	1-----1112--1	-----	------2
Pisidium henslowanum	--111-	11--1--	-1----1	--1--	1-11--------1	-----	2111---
Manayunkia speciosa	--11--	----1--	-------	-----	-----2--1----	-----	-------
Uncinais uncinata	-1----	1-1----	----1--	-----	-----2-----1-	-----	-------
Chironomus salinarius	-1-1-1	-------	1------	-----	---------1--1	11--1	--1----
Valvata sincera	-1-1-1	1-11111	-1----3	-----	3-12-211-----	-3---	2211---
Sphaerium nitidum	-11111	-111121	-1-1---	-1--3	1-21-11-----2	-----	2121-11
Pisidium subtruncatum	-1-1--	1------	-------	-----	-11------1---	-----	3------
Slavina appendiculata	--1-31	-11-111	11-1-1-	---21	1---1-1121-62	11---	---12--
Aulodrilus pluriseta	-31---	-------	-------	-----	1-----1-3----	-----	11-1---
Piona	--1-11	11--121	--11111	---33	1-11-3--2-222	-11--	--1----
Cryptochironomus	-1---1	11-1---	1-11111	--1--	--11-----11-1	11322	-------
Micropsectra	------	111----	-12----	21212	1-11--111-112	-----	------2
Heterotrissocladius changi	-1--12	1131---	1121122	35421	1111--12--3-4	-1-2-	-----11
Pisidium ventricosum	------	1------	-1-----	-----	-1-1--1--1---	-----	-------
Vejdovskyella intermedia	1-----	-1--1-1	--13211	-3234	1-21221-13455	-1-16	---122-
tubificids (imm. with hs)	-21-11	11--112	-111-11	--131	33133-4543123	-313-	---1-23
Diaporeia	------	-----11	--1----	2-1-1	-35-54---21-2	-----	------3
Chironomus anthracinus	-1--1-	-------	---1---	-----	-1-1--1---1-1	12311	-------
Polypedilum laetum	------	-------	----1--	--111	--1-------1-1	-----	-------
Polypedilum scalaenum	------	-----1-	-------	-----	-------------	--234	-------
Pisidium casertanum	-11222	2111223	1111115	-13-4	424521433224-	31---	-123341
Pisidium ferrugineum	----1-	----11-	--1----	1---1	1------------	-----	4353-31
Pisidium lilljeborgi	-1-1--	1--1221	-1-1-11	143-2	11231311--1--	2-2--	5342334
Stylodrilus heringianus	1-1121	21-111-	1111-11	61332	3334-3-11-111	-1---	3535535
Limnodrilus hoffmeisteri	-1---1	------1	-----1-	1--11	1-111-12-----	-----	-13--1-
Potamothrix moldaviensis	-1----	----1--	--1---1	---1-	-----1-1-----	-131-	---1122
Potamothrix vejdovskyi	-1-111	-----11	--1----	---21	31-1--3321---	12-2-	-11343-
Spirosperma ferox	-11321	1---131	-111-1-	---12	1133422223-1-	-111-	23331-1
Tubificid embryos	----1-	-----1-	-------	-----	------1-11---	1----	--1--1-
tubificids (imm. wo hs)	141113	1---113	1133113	1-132	4623345332413	84353	-332353

Sample Group	GR#1	GR#2	GR#3	GR#4	GR#5	GR#6	GR#7
Number of Samples	6	7	7	5	13	5	7
Number of Taxa	41.5	51.8	43.4	33.8	27.1	22.4	16.7
Shannon Diversity	3.4	3.6	3.8	3.1	3.2	2.7	2.3
Total Individuals	46257	41084	61301	30923	18331	10730	19169
Number of Samples							
Rock	6	6	5	3	5	1	0
Gravel/Sand	0	1	1	2	4	3	2
Silt/Clay	0	0	1	0	4	1	5
Summary Groups (#/m2)							
Ephemeroptera	1	40	728	0	0	0	6
Trichoptera	158	1151	320	144	10	0	0
Coleoptera	0	0	24	0	0	0	0
Isopoda	102	1420	1104	824	185	39	18
Acarina	748	1973	1673	2522	577	68	6
Hydrozoa	40	3560	3	1019	114	1	0
Nemertea	0	6	85	0	0	17	0
Turbellaria	673	1887	1157	17	46	1	0
Amphipoda	17235	9372	15717	328	2330	166	564
Decapoda	35	38	24	0	0	0	0
Hirudinea	20	124	139	0	18	3	0
Chironomini	189	1852	5442	468	615	1143	12
Diamesinae	24	2	227	62	39	10	0
Tanytarsini	324	1712	12030	2049	1054	619	61
Orthocladiinae	349	422	4975	1542	446	309	61
Tanypodinae	90	761	1427	346	105	1	36
Gastropoda	15632	9115	6705	798	500	469	643
Dreissenidae	1197	8	10	0	3	0	30
Sphaeriidae	1495	2944	1897	4513	2674	1043	5369
Polychaeta	6	106	0	0	33	0	0
Enchytraeidae	0	192	0	0	0	0	0
Lumbriculidae	535	141	396	3354	1062	11	6265
Naididae	5385	779	6073	4488	3893	1230	198
Tubificidae	1889	3407	1732	3365	4718	5659	5300
Chironomidae	975	4749	24102	4306	2703	2082	170
Oligochaeta	7808	4559	8202	12207	9674	6900	11762
Bivalvia	2693	2976	1907	8513	2677	1043	5599

Note: The abundance rankings of taxa in samples were based on percent contribution of sample total and are as follows 0. not present: 1. 0-2%. 2. >2-5%: 3. >5-15%: 4. >15-25%. 5. >25-50%: >50-100%

Table 14. Results from ANOVAs testing for differences in mean ordination (Correspondence Analysis) axis scores among fetch zones at 5 and 20 m and in 1991.

CA axis	Source	df	SS	MS	F	P
5 m						
1	fetch	2	2.187	1.094	4.784	0.019
	error	22	5.029	0.229		
2	fetch	2	1.289	0.645	4.448	0.024
	error	22	3.188	0.145		
3	fetch	2	2.102	1.051	2.573	0.099
	error	22	8.985	0.408		
20 m						
1	fetch	2	0.151	0.075	0.498	0.615
	error	22	3.327	0.151		
2	fetch	2	4.016	2.008	5.463	0.012
	error	22	8.087	0.368		
3	fetch	2	0.692	0.346	1.819	0.186
	error	22	4.182	0.190		

Table 15. Average density (No. m^{-2}) of bivalves collected as part of the macro-benthos survey. Transect numbers are given. All samples were collected from 5 m.

Taxon	Transect							
	1	2	3	4	5	7	8	9
Dreissena polymorpha	24454	18404	8884	2832	742	611	189	1644
Dreissena sp.	27	111	19	3	0	0	3	3
Musculium sp.	70	0	0	3	0	0	0	0
Sphaerium sp.	96	2	6	195	0	2	0	10
Pisidium sp.	96	11	9	284	0	2	0	0
Unionidae	0	0	0	3	0	0	0	0

Table 16. Summary of bivalve taxa contributing to structure of Correspondence Analysis axes describing structure of bivalve communities from 5 m at 8 transects in Lake Ontario between Toronto and Niagara-On-The-Lake. Summary is based on information in Appendix G.

Axis	Taxon	Contribution to Axis	Squared Correlation with Axis
1	*Sphaerium nitidum*	0.285	0.906
	Pisidium fallax	0.260	0.694
2	*Sphaerium striatinum*	0.163	0.400
	Pisidium lilljeborgi f. *cristatum*	0.253	0.748
	Unionidae	0.126	0.748
3	*Musculium transversum*	0.111	0.634

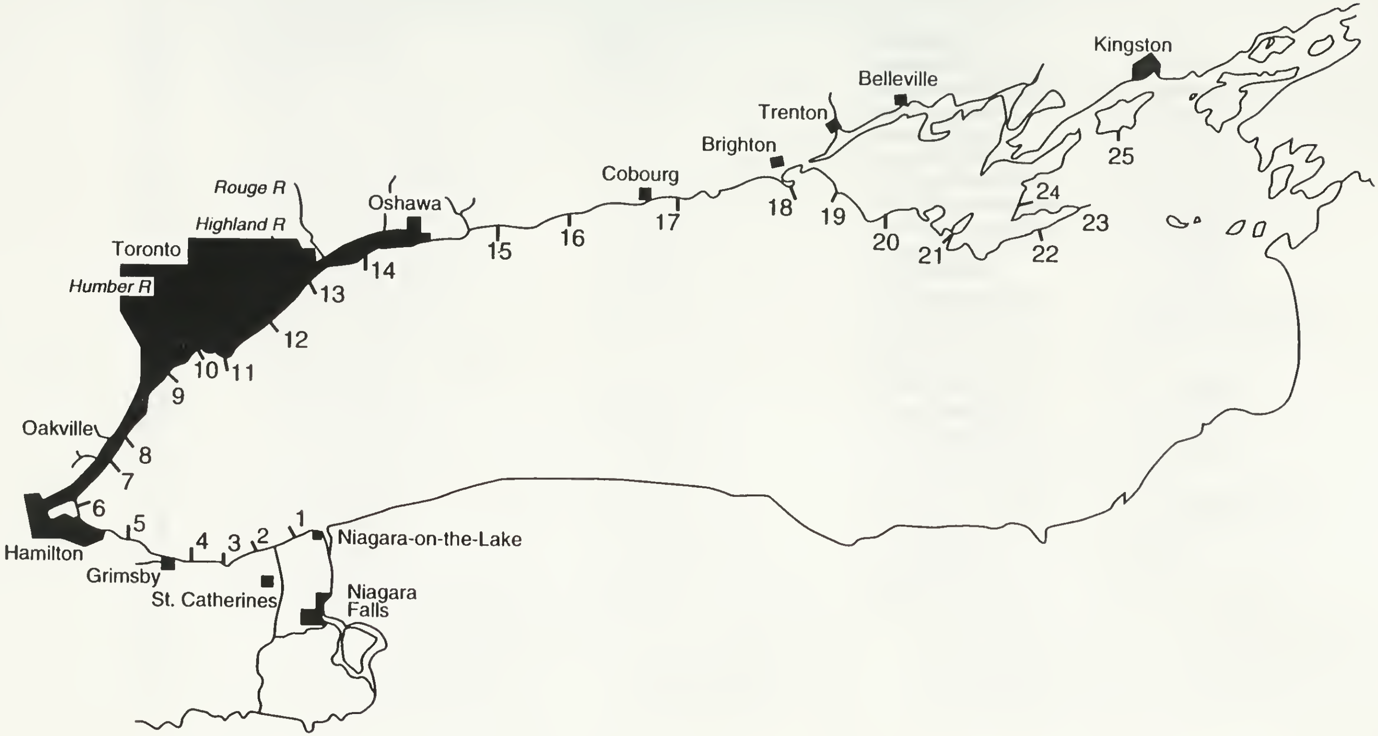

Figure 1. Map of Lake Ontario showing the distribution of transects from Niagara-On-The-Lake to Amherst Island.

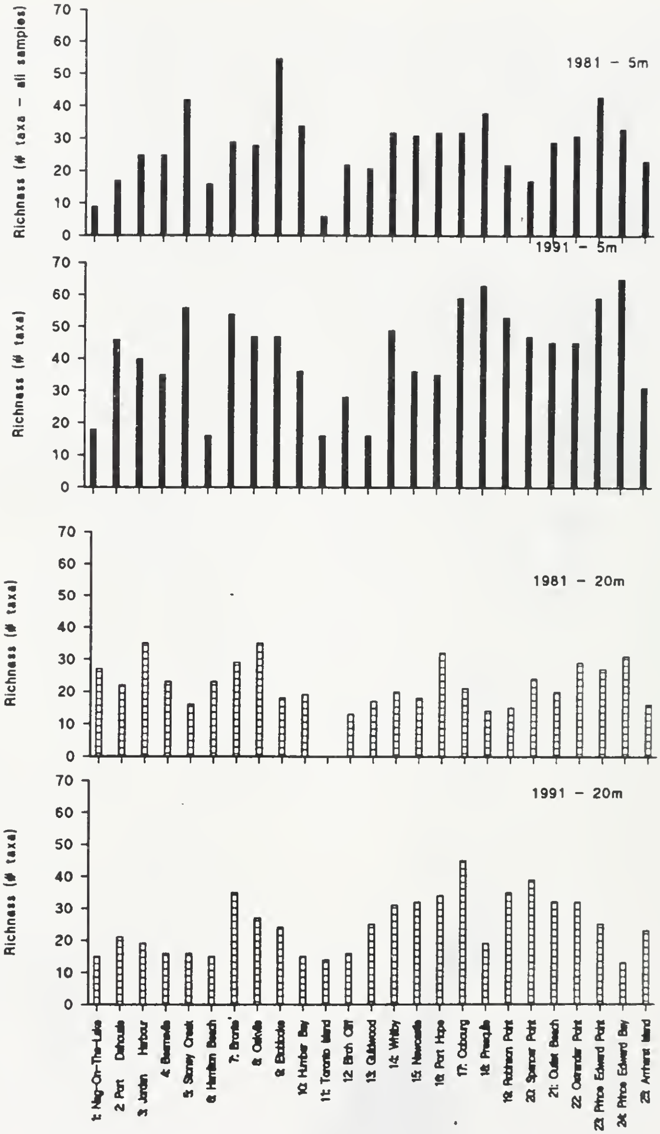

Figure 2. Histograms showing taxonomic richness at each transect and depth in 1981 and 1991.

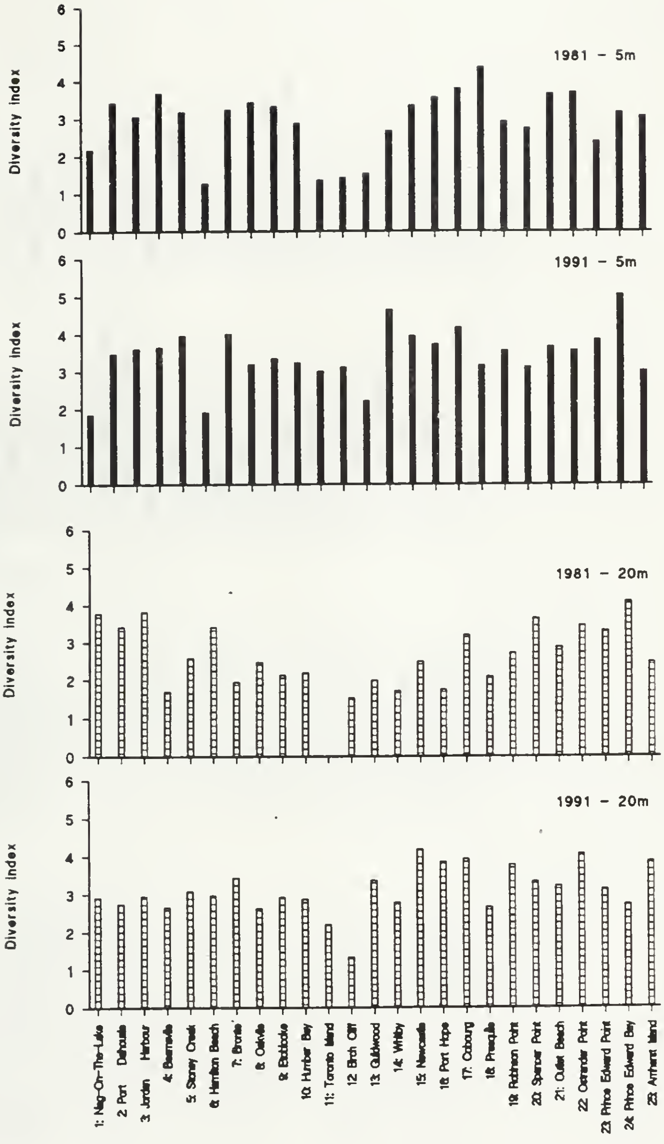

Figure 3. Histograms showing Shannon H' values at each transect and depth in 1981 and 1991.

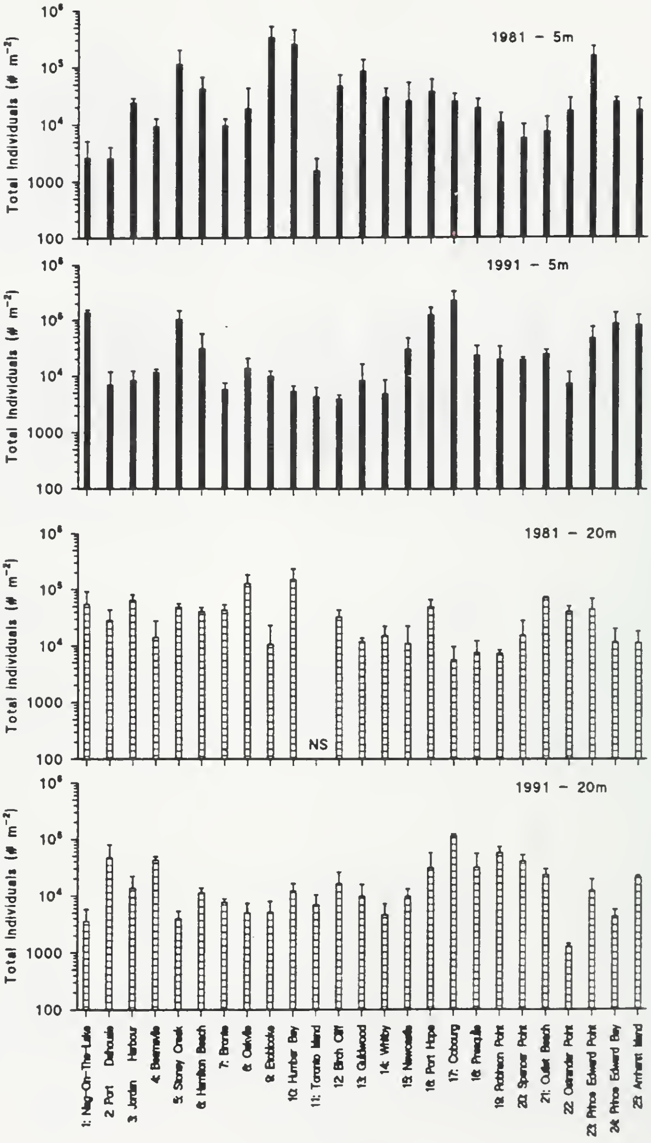

Figure 4. Histograms showing total density (No. m^{-2}) of macroinvertebrates at each transect and depth in 1981 and 1991.

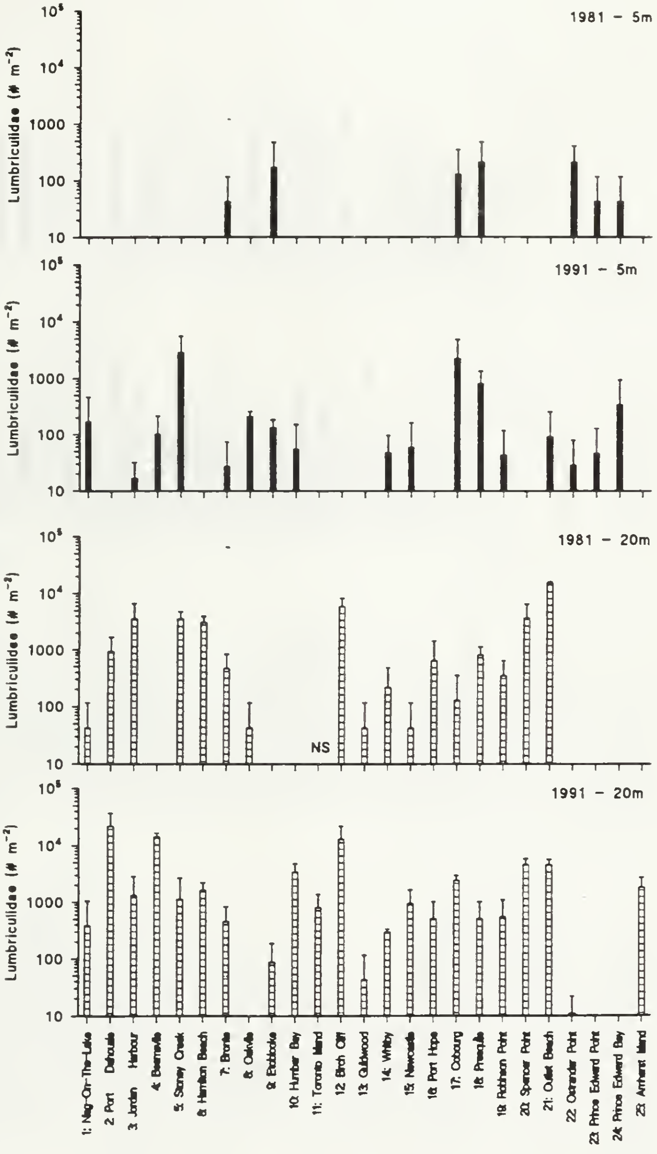

Figure 5. Histograms showing density (No. m^{-2}) of Lumbriculidae at each transect and depth in 1981 and 1991.

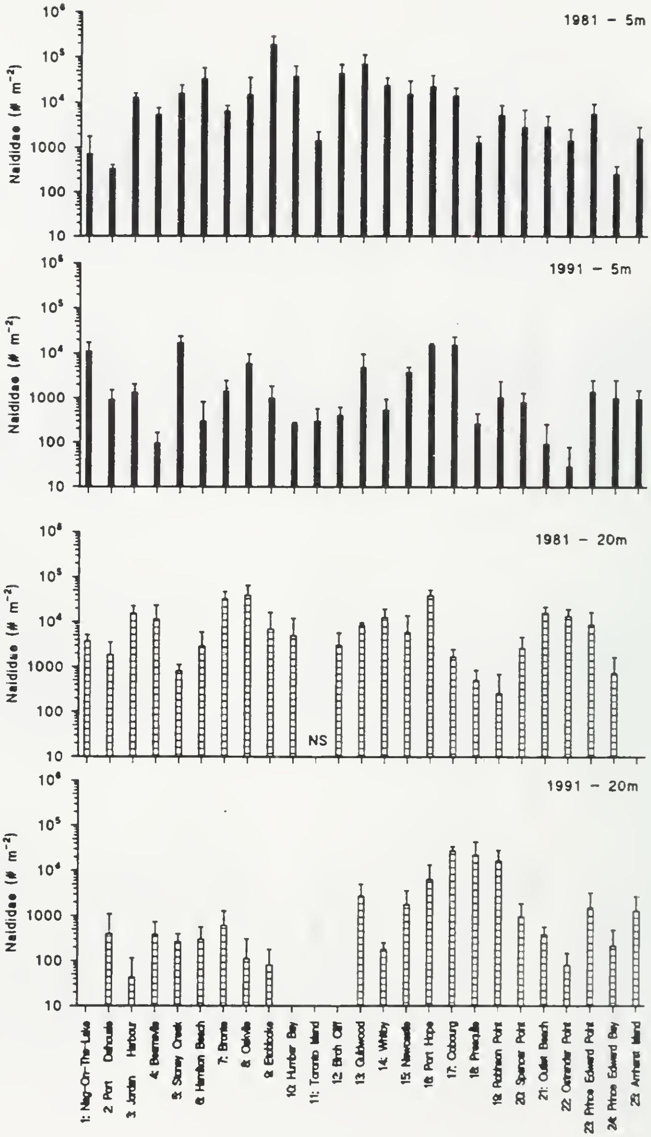

Figure 6. Histograms showing density (No. m^{-2}) of Naididae at each transect and depth in 1981 and 1991.

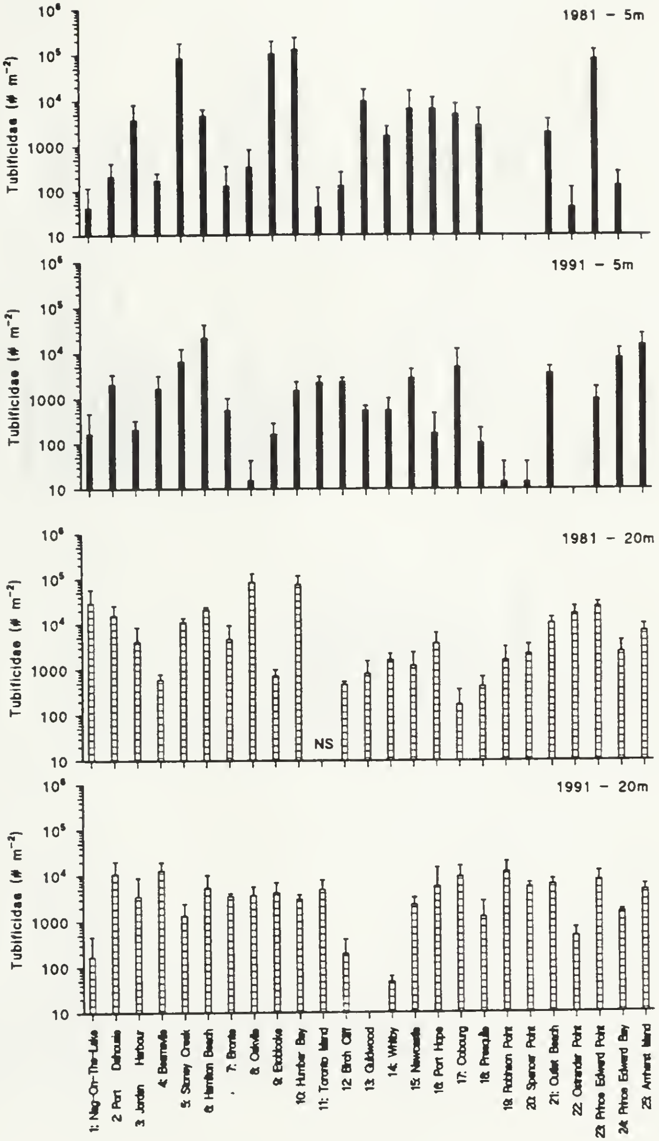

Figure 7. Histograms showing density (No. m^{-2}) of Tubificidae at each transect and depth in 1981 and 1991.

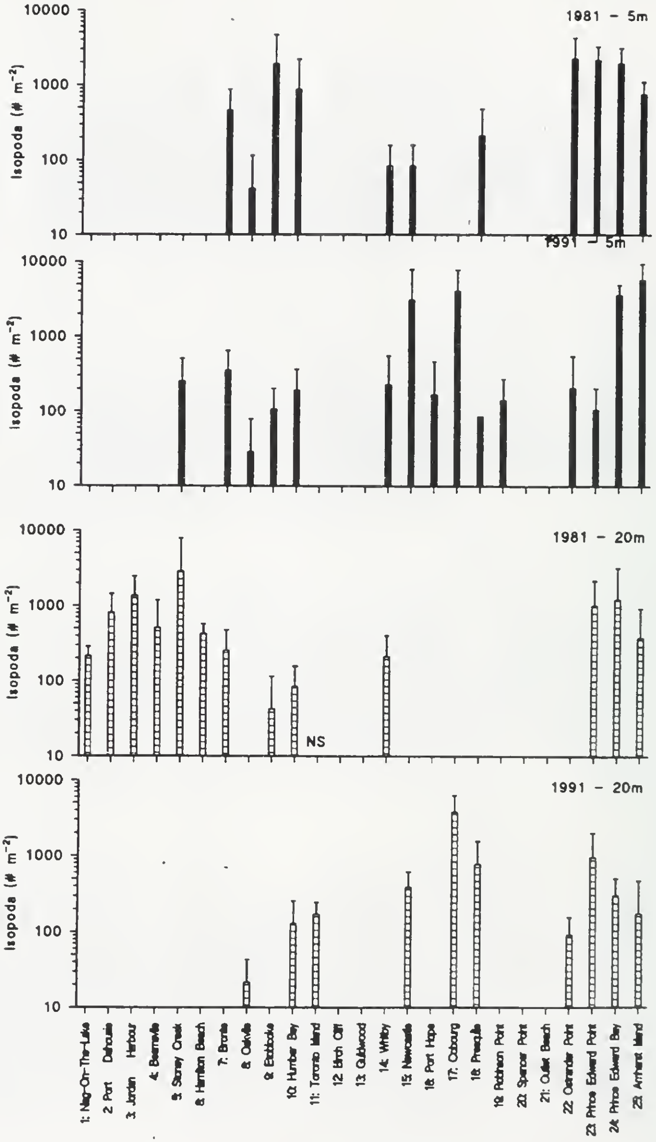

Figure 8. Histograms showing density (No. m^{-2}) of Isopoda at each transect and depth in 1981 and 1991.

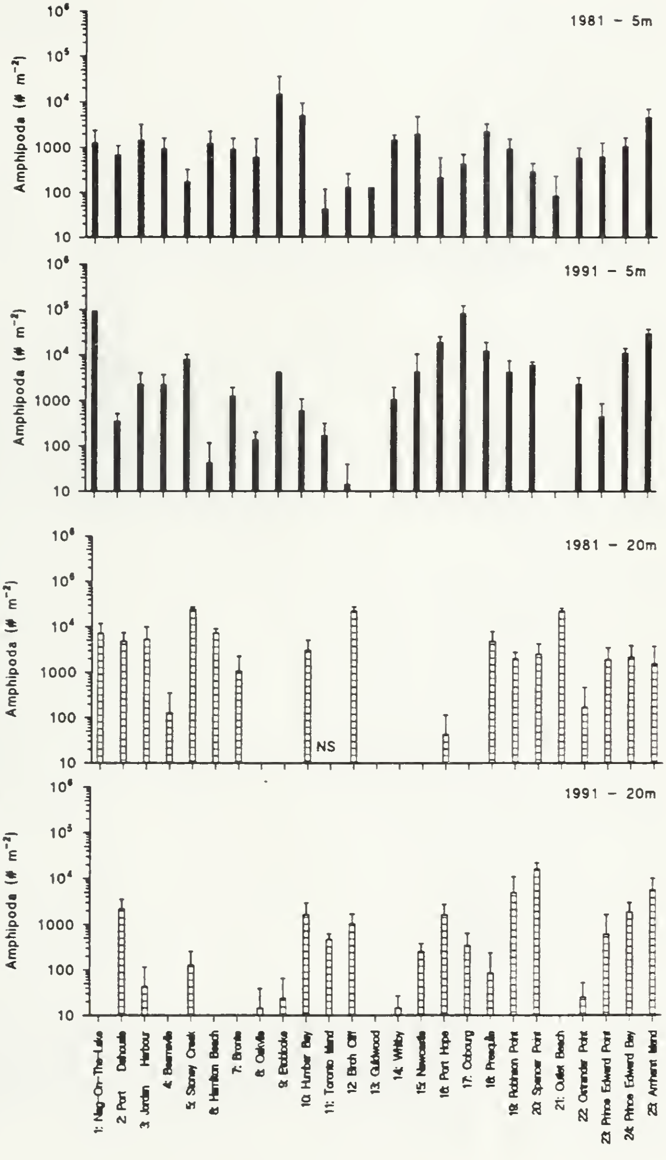

Figure 9. Histograms showing density (No. m^{-2}) of Amphipoda at each transect and depth in 1981 and 1991.

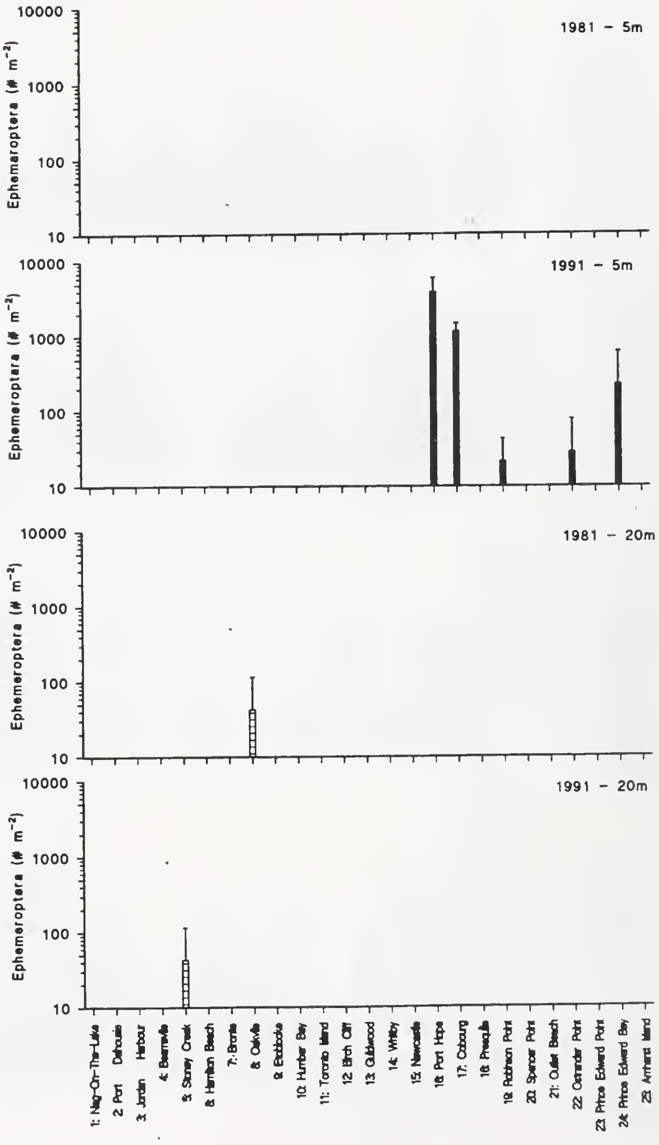

Figure 10. Histograms showing density (No. m^{-2}) of Ephemeroptera at each transect and depth in 1981 and 1991.

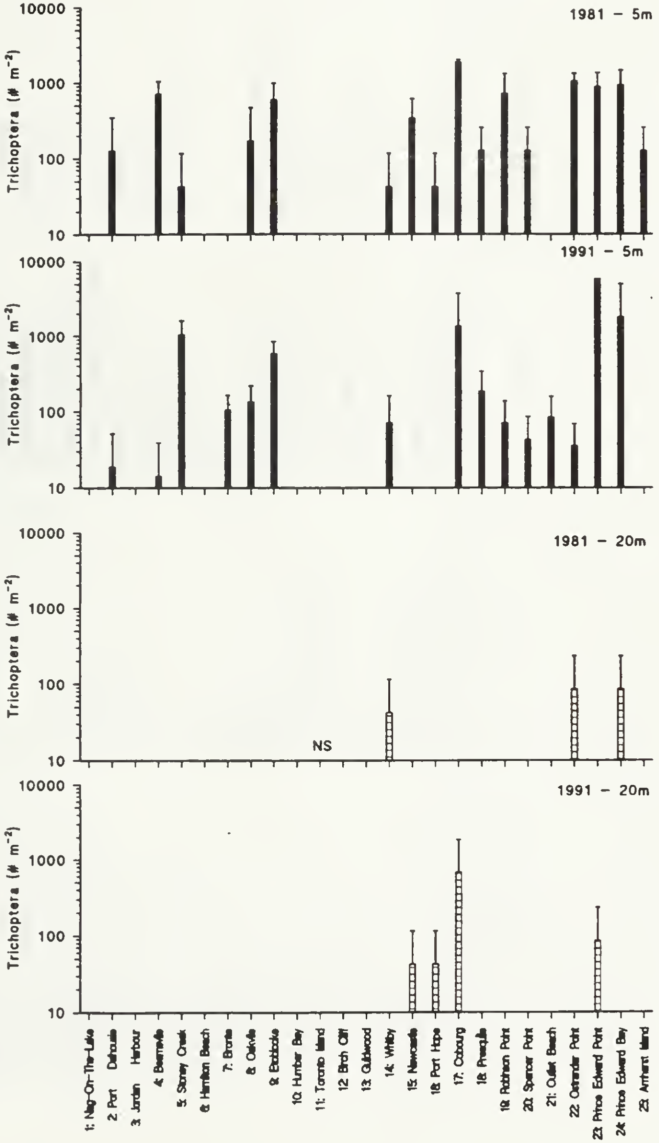

Figure 11. Histograms showing density (No. m^{-2}) of Trichoptera at each transect and depth in 1981 and 1991.

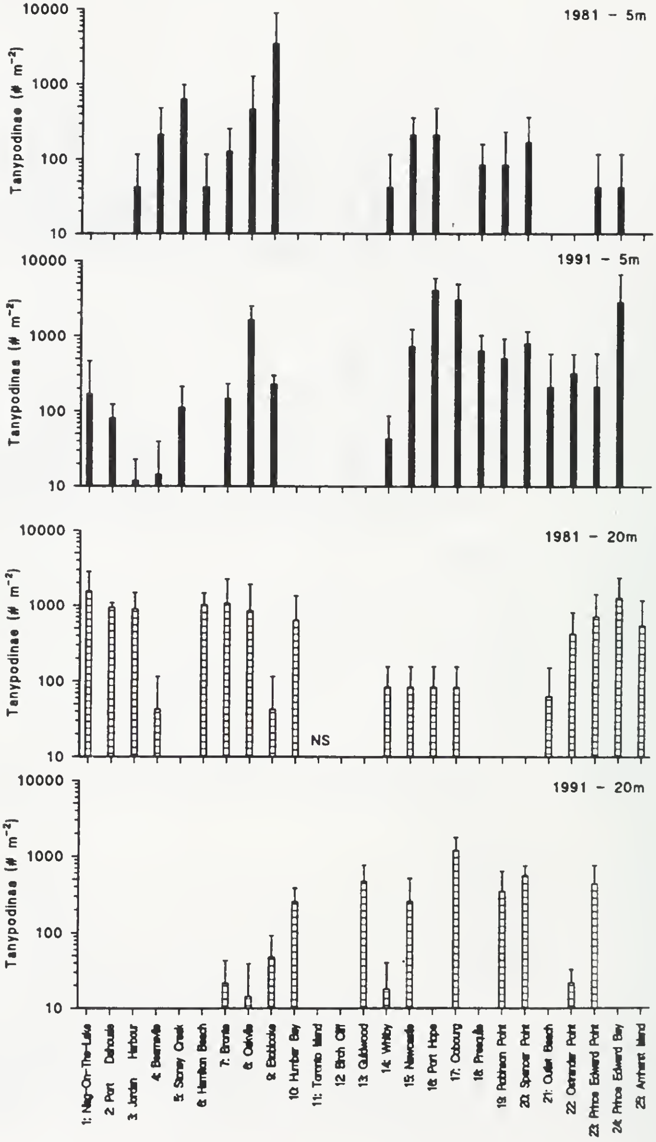

Figure 12. Histograms showing density (No. m^{-2}) of Tanypodinae at each transect and depth in 1981 and 1991.

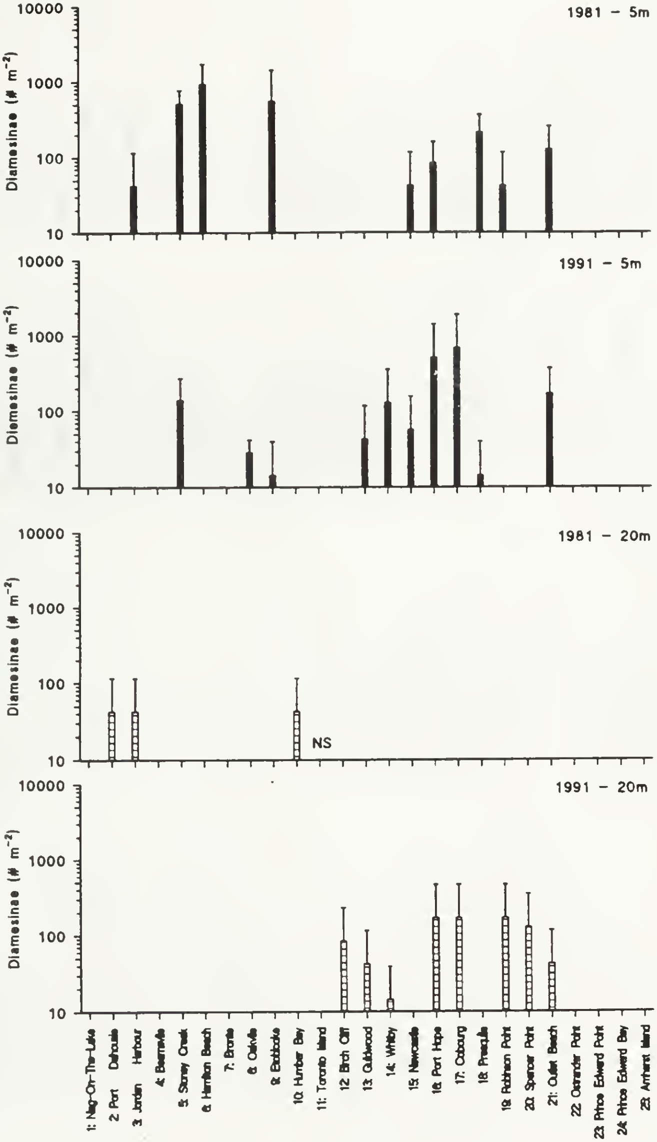

Figure 13. Histograms showing density (No. m^{-2}) of Diamesinae at each transect and depth in 1981 and 1991.

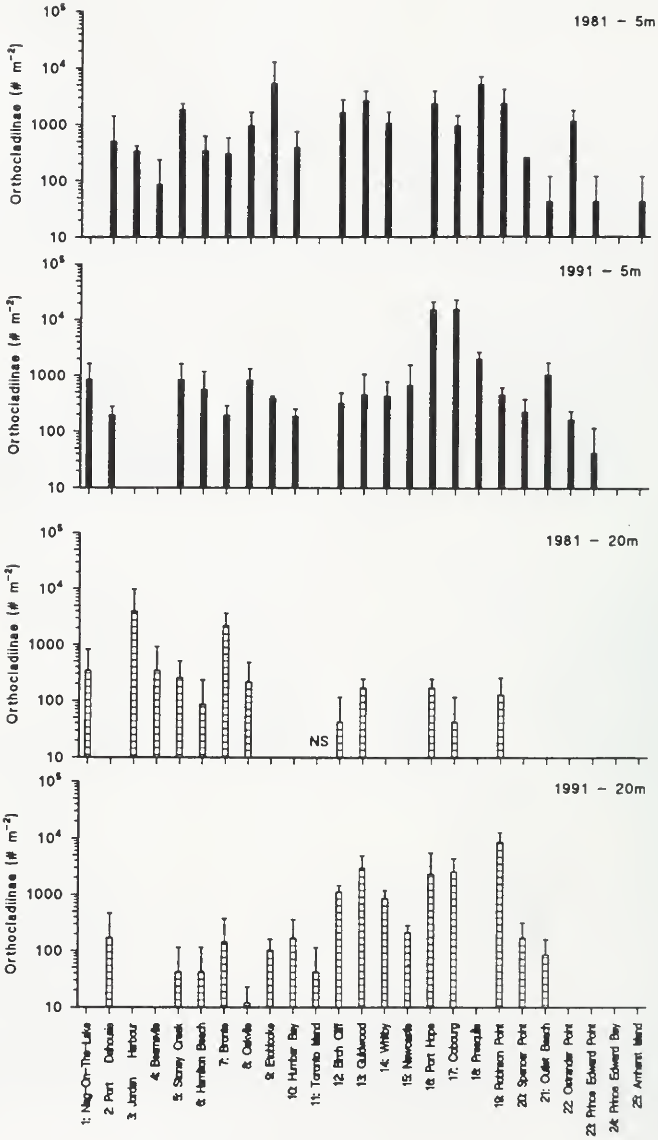

Figure 14. Histograms showing density (No. m^{-2}) of Orthocladiinae at each transect and depth in 1981 and 1991.

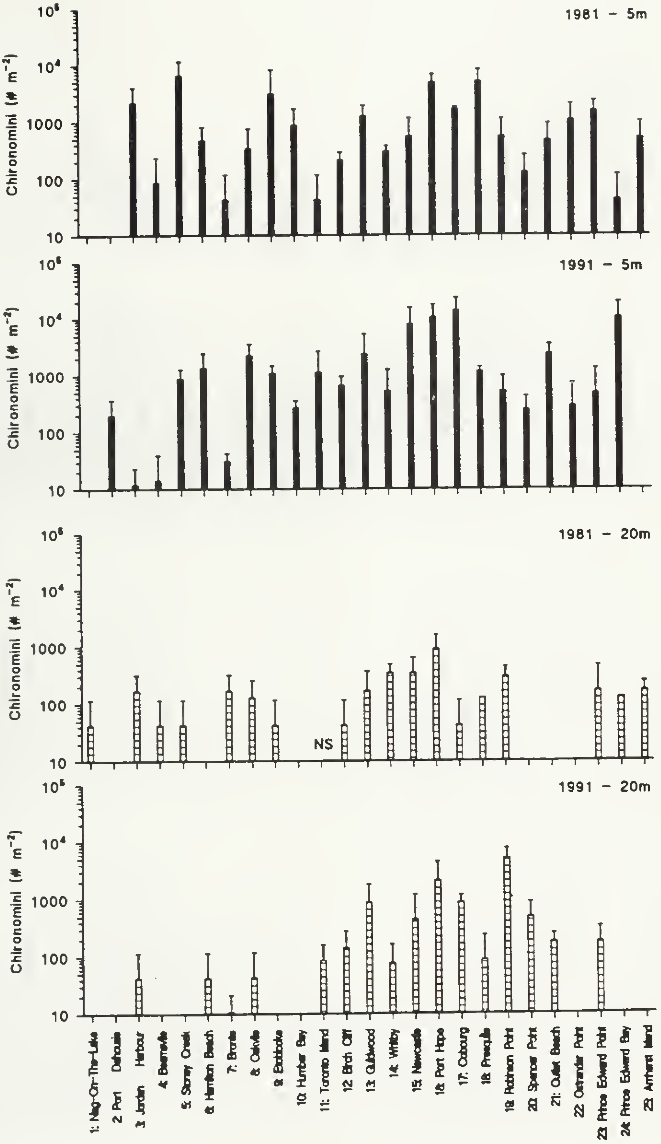

Figure 15. Histograms showing density (No. m^{-2}) of Chironomini at each transect and depth in 1981 and 1991.

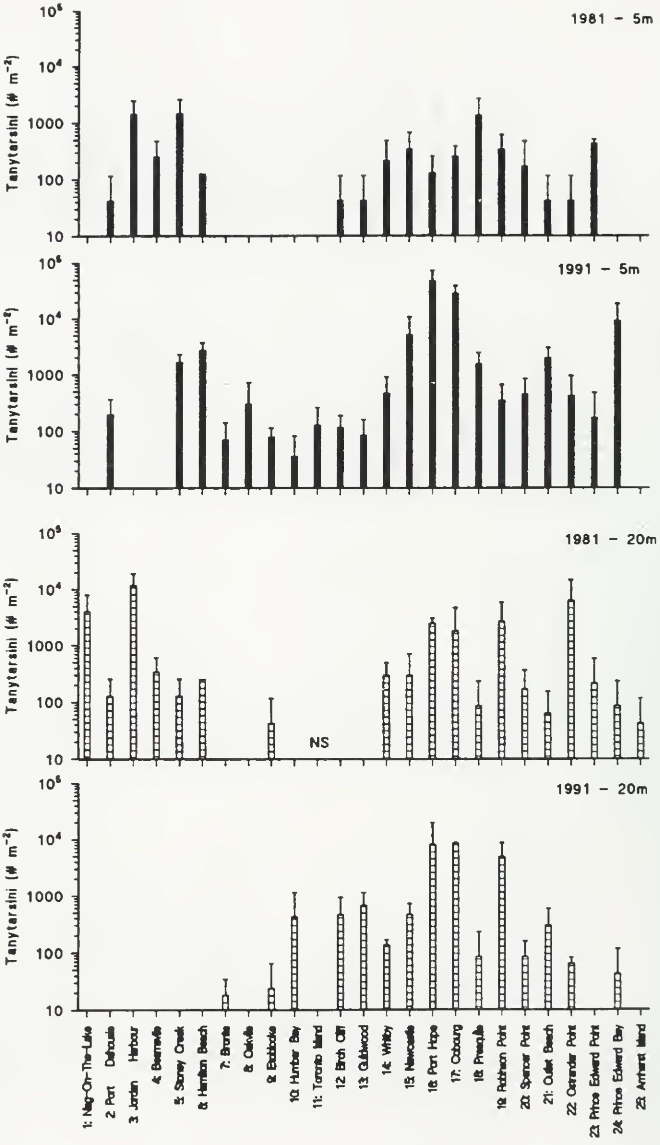

Figure 16. Histograms showing density (No. m^{-2}) of Tanytarsini at each transect and depth in 1981 and 1991.

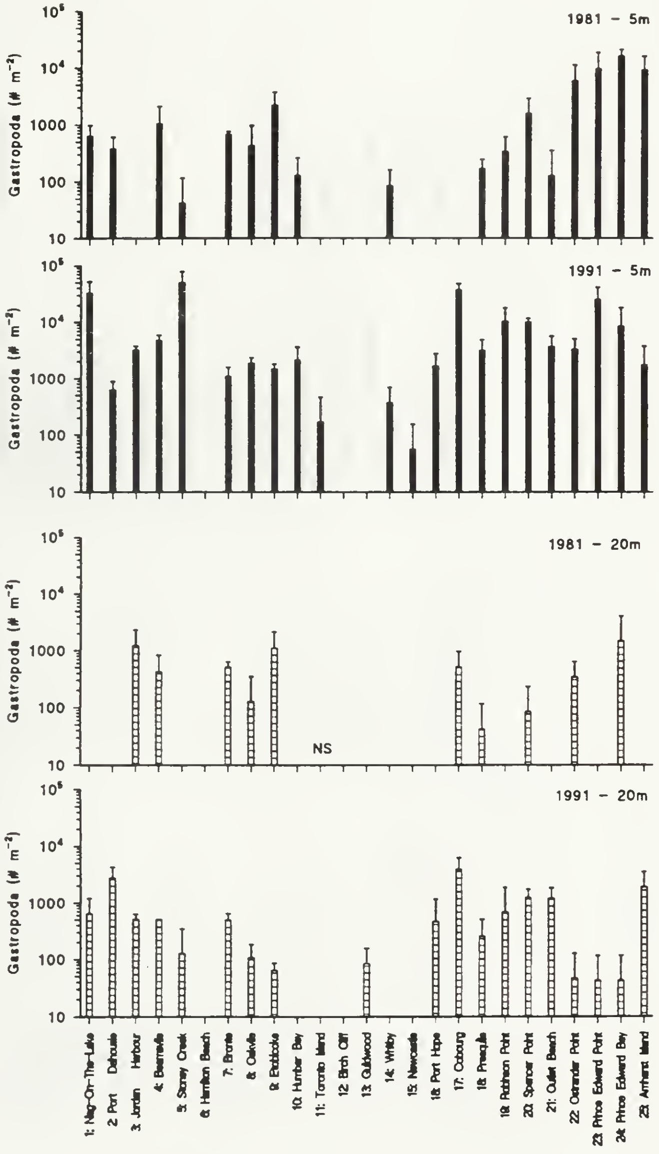

Figure 17. Histograms showing density (No. m^{-2}) of Gastropoda at each transect and depth in 1981 and 1991.

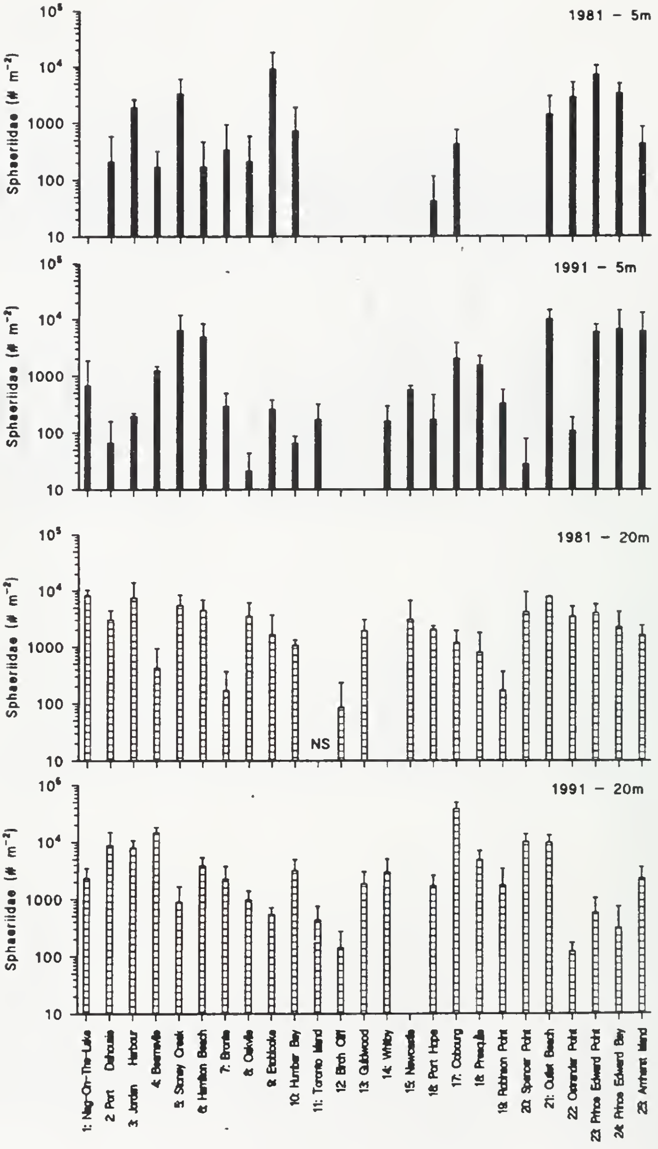

Figure 18. Histograms showing density (No. m^{-2}) of Sphaeriidae at each transect and depth in 1981 and 1991.

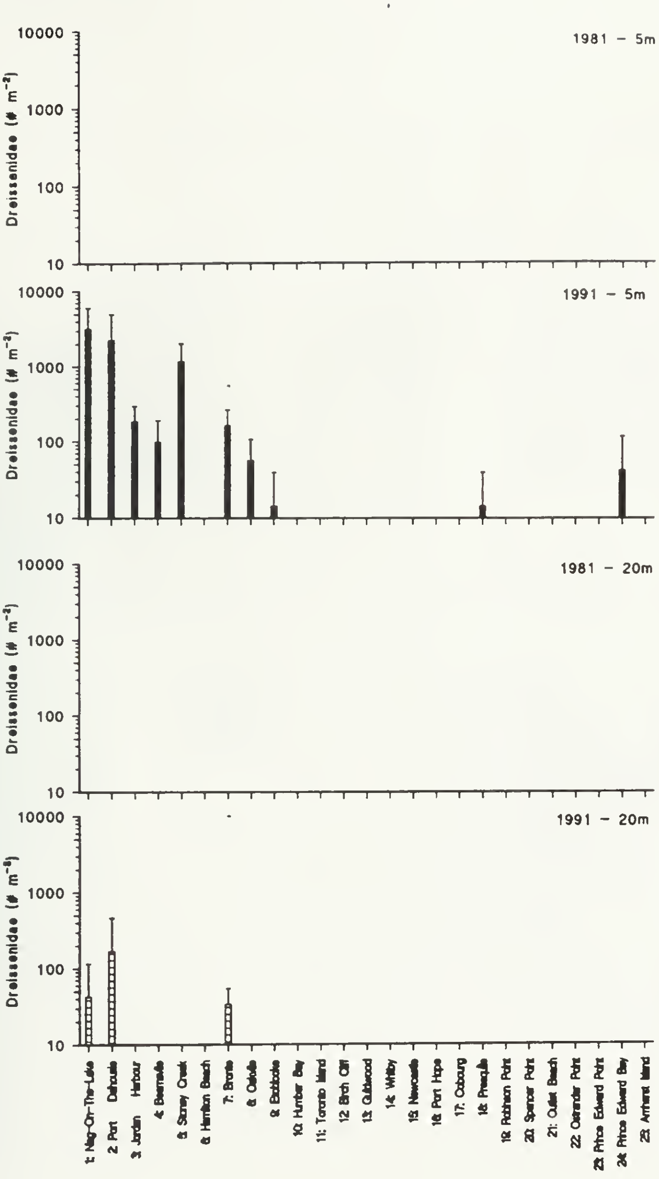

Figure 19. Histograms showing density (No. m^{-2}) of zebra mussels at each transect and depth in 1981 and 1991.

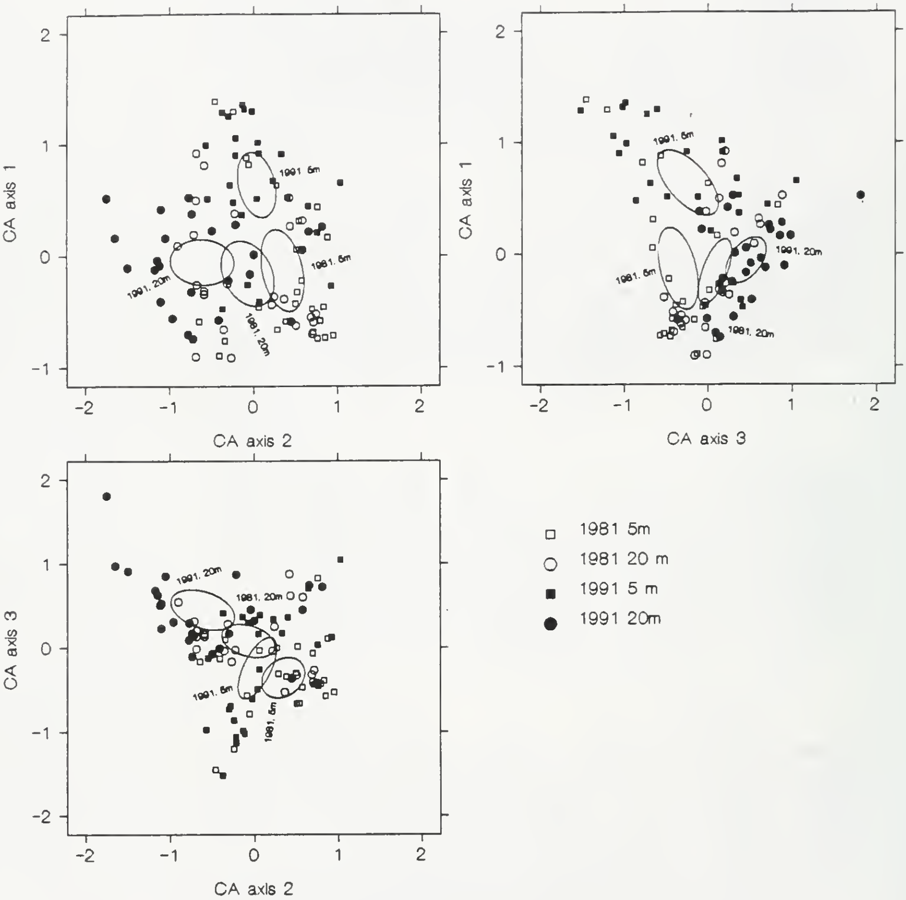

Figure 20. Scatterplot of Correspondence Analysis (CA) sample scores. CA was based on benthic samples collected from Lake Ontario at 5 and 20 m, during 1981 and 1991 at 25 transects.

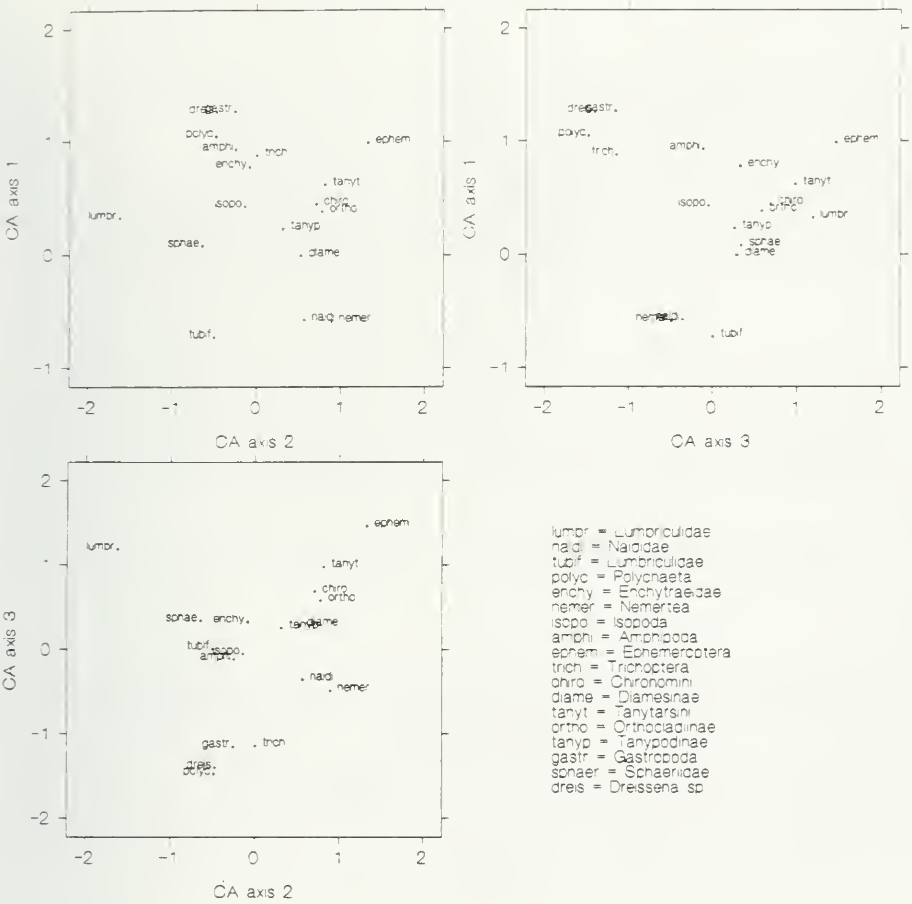

Figure 21. Scatterplot of Correspondence Analysis (CA) taxa scores. CA was based on benthic samples collected from Lake Ontario at 5 and 20 m, during 1981 and 1991 at 25 transects.

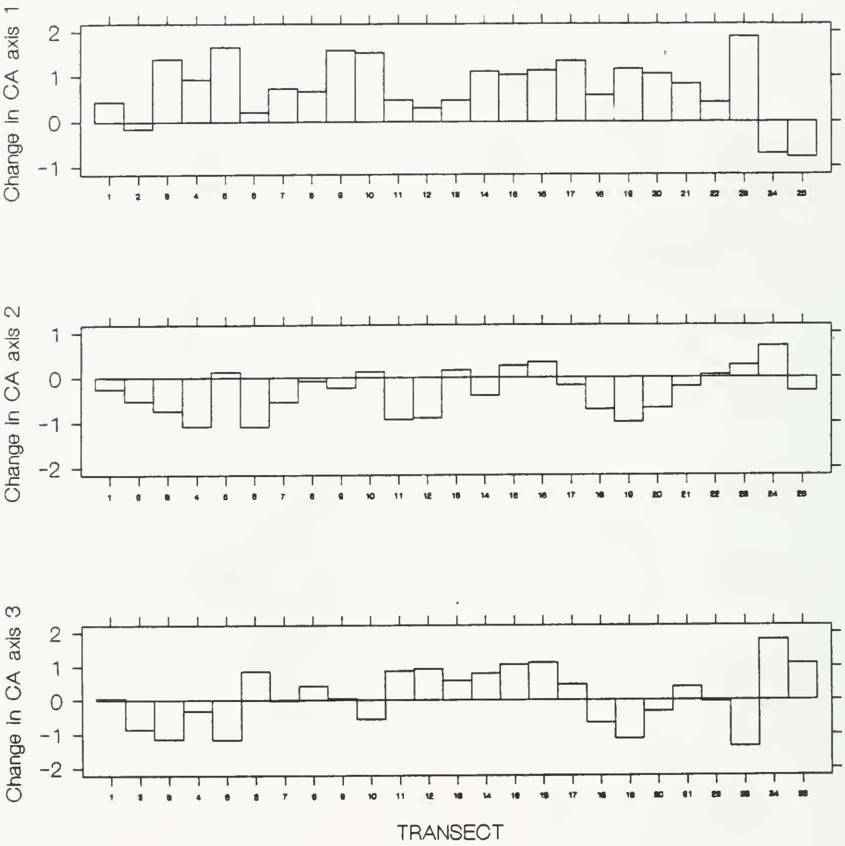

Figure 22. Histograms showing the mean change in ordination (Correspondence Analysis of major taxonomic groups) axis scores from 1981 to 1991 at 5 m in Lake Ontario.

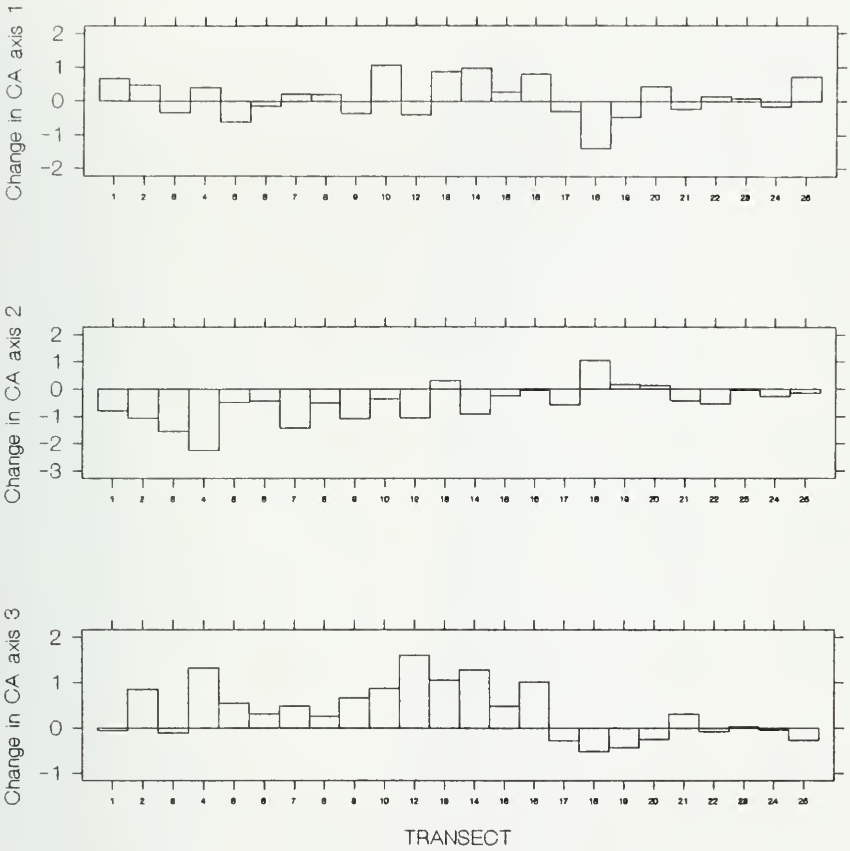

Figure 23. Histograms showing the mean change in ordination (Correspondence Analysis of major taxonomic groups) axis scores from 1981 to 1991 at 20 m in Lake Ontario.

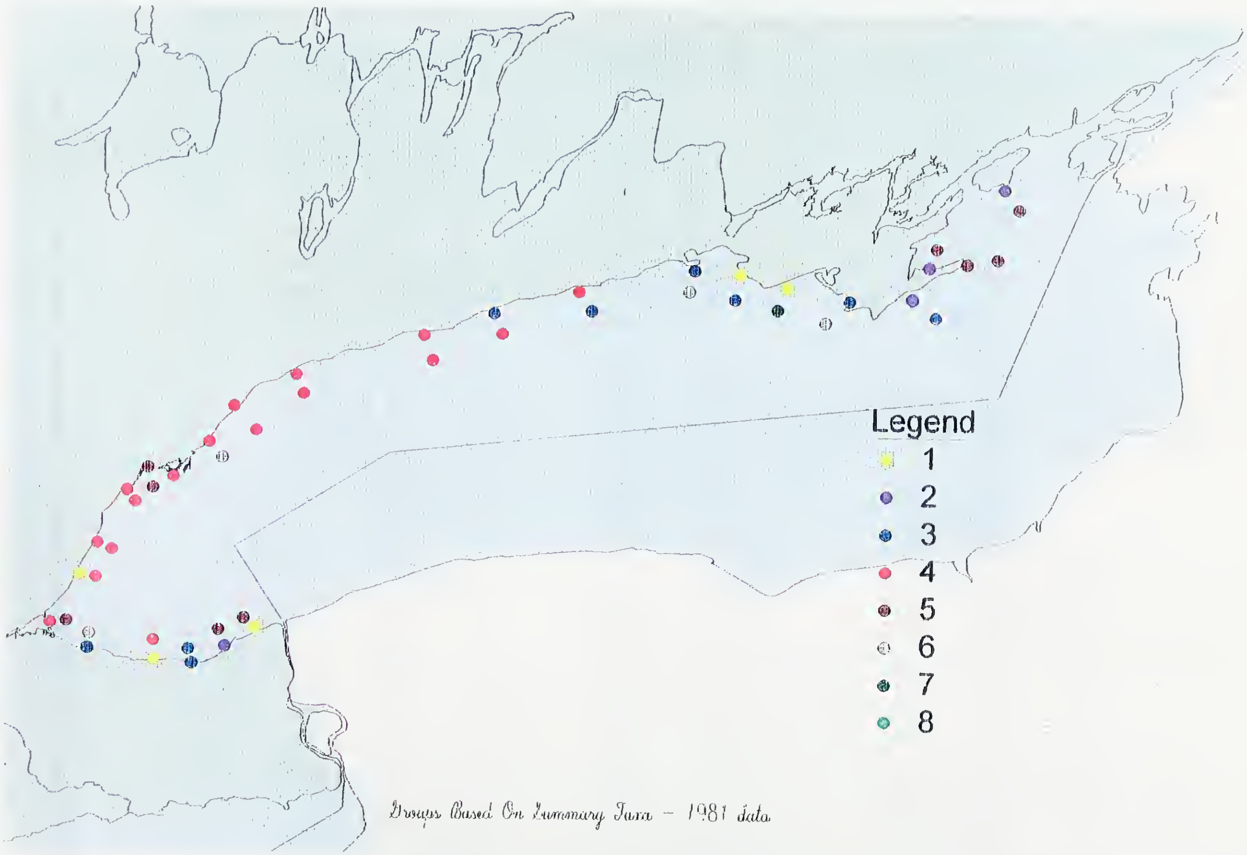

Figure 24. Map of Lake Ontario showing the 1981 TWINSPAN groupings at 5 and 20 m in Lake Ontario. TWINSPAN was based on major taxonomic groups.

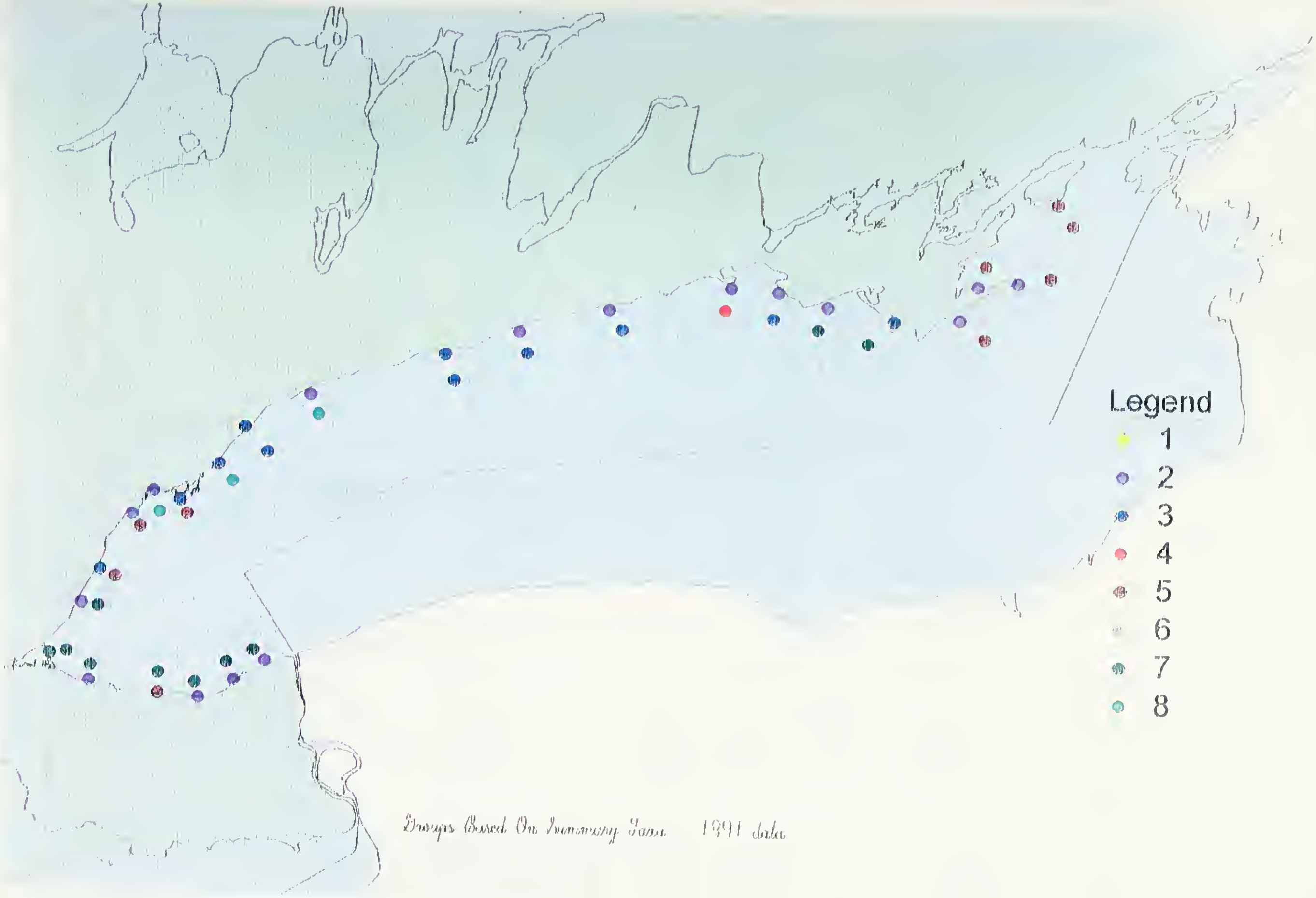

Figure 25. Map of Lake Ontario showing the 1991 TWINSPAN groupings at 5 and 20 m in Lake Ontario. TWINSPAN was based on major taxonomic groups.

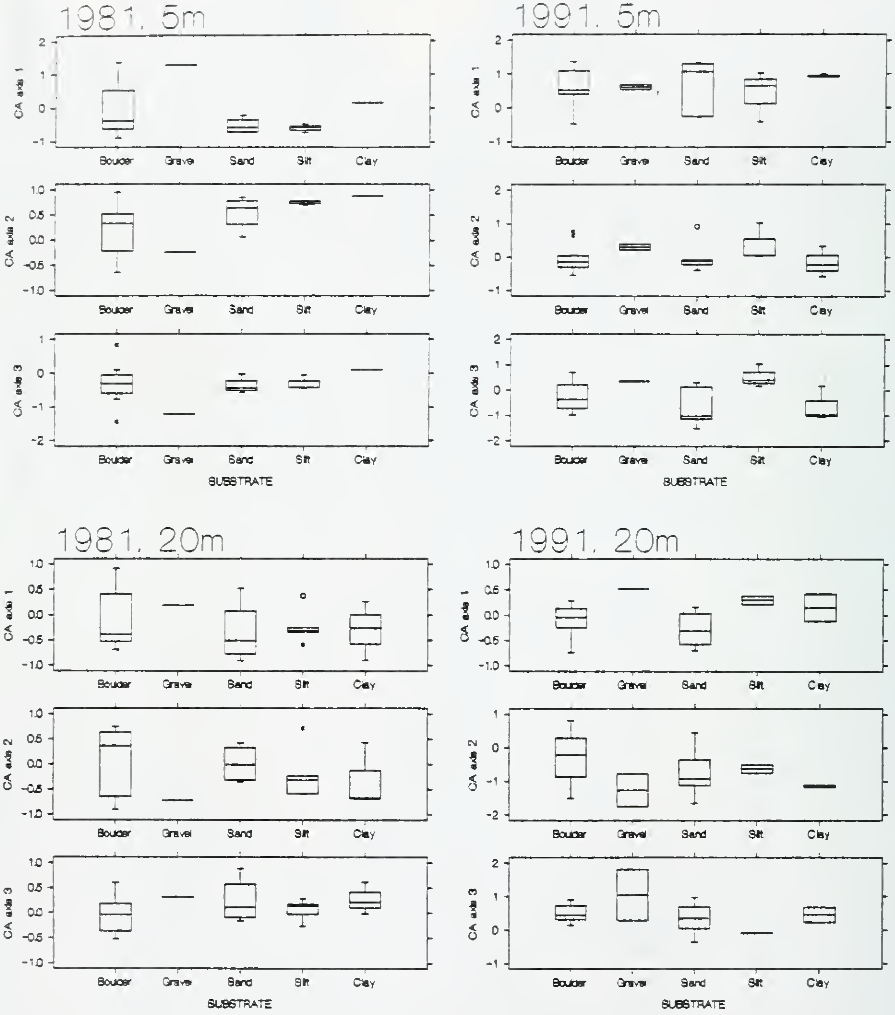

Figure 26. Box plots of CA axis scores for each substrate class within each depth and year combination.

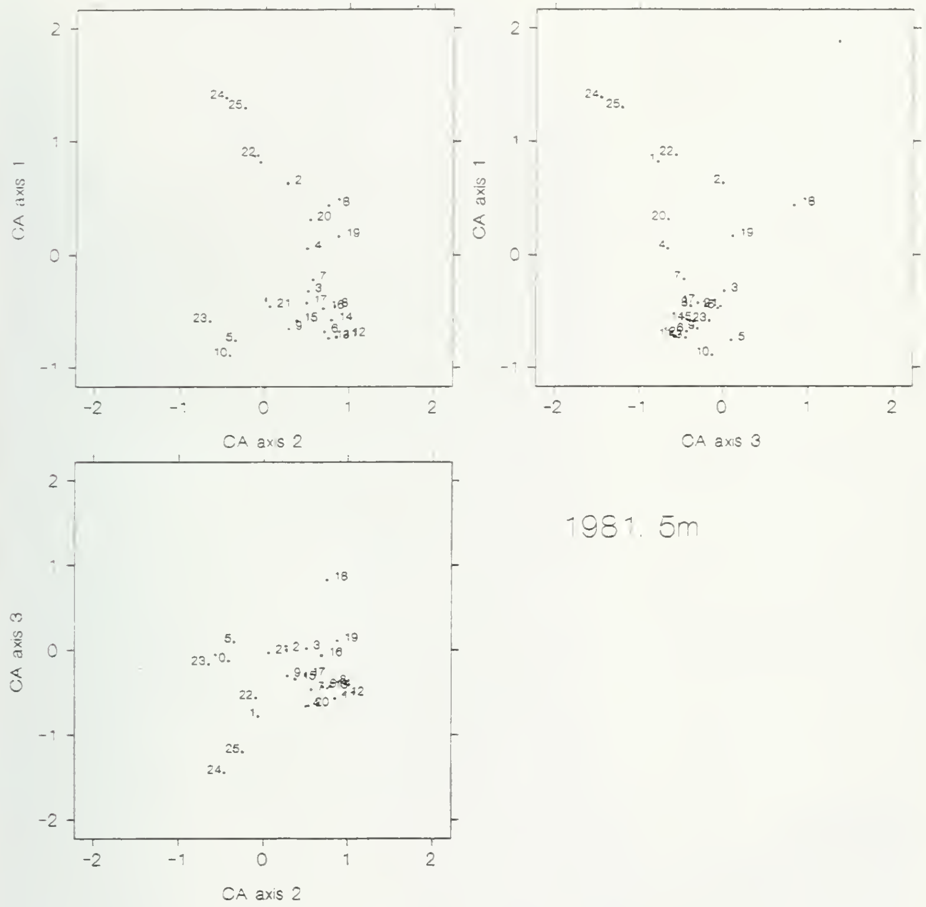

Figure 27. Scatterplot of CA axis scores in 1981 at 5 m. Transect are labelled to illustrate the association between proximity of transects and similarity of communities.

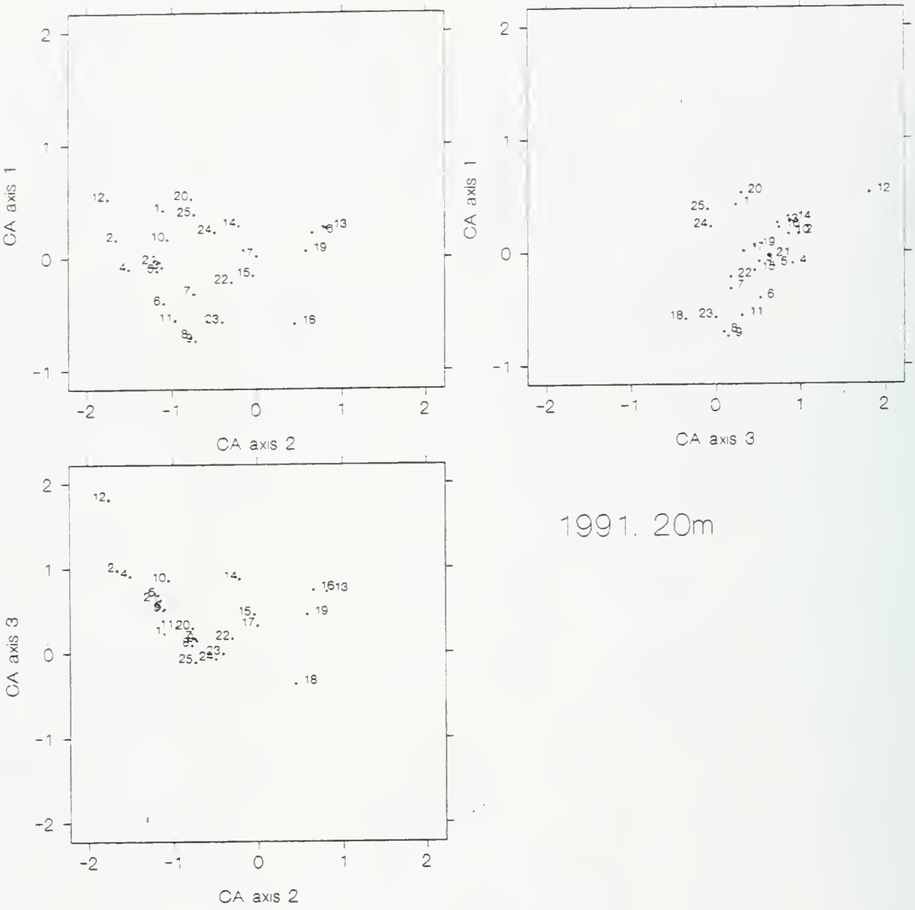

Figure 28. Scatterplot of CA axis scores in 1991 at 20 m. Transect are labelled to illustrate the association between proximity of transects and similarity of communities.

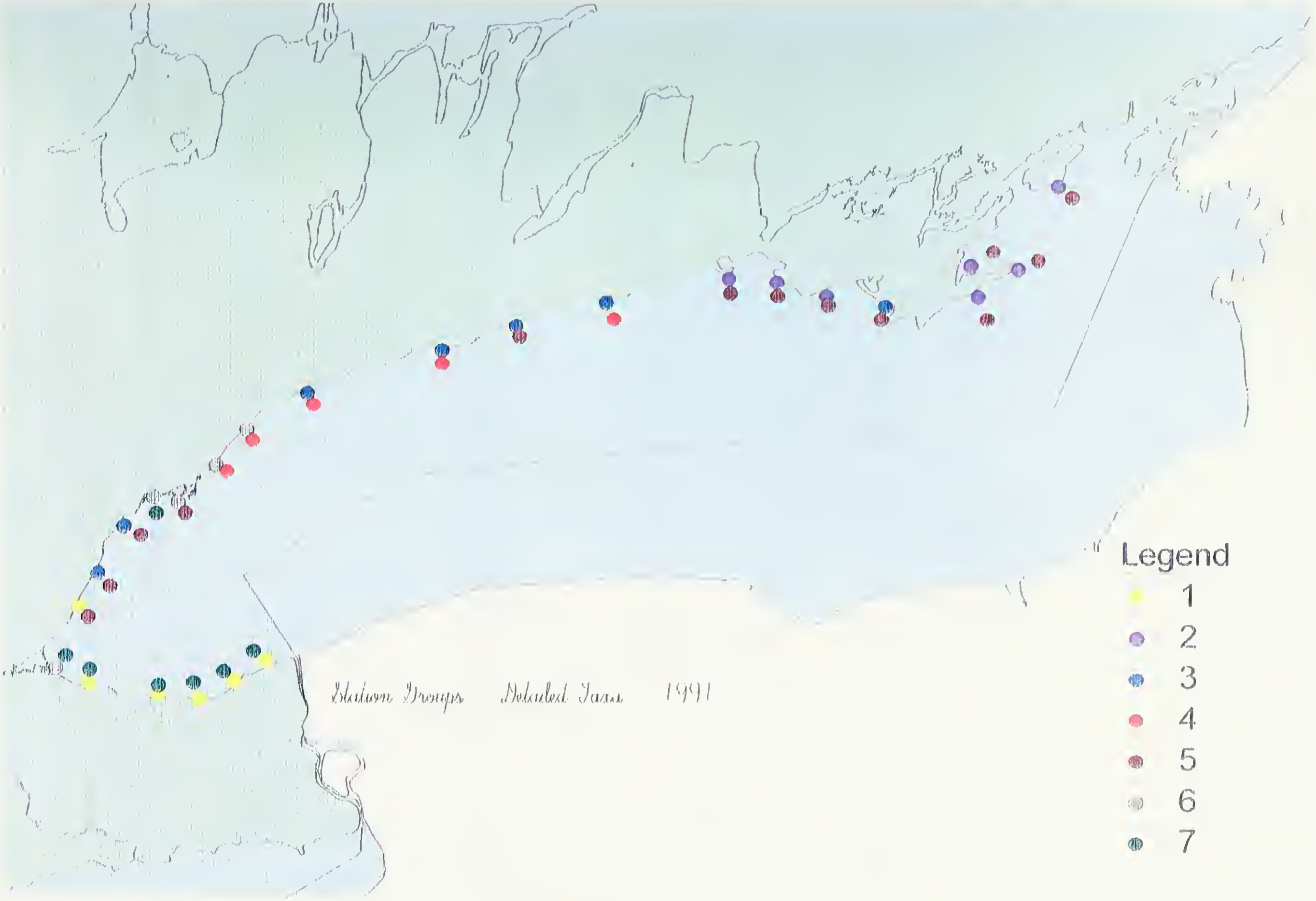

Figure 29. Map of Lake Ontario showing the 1991 TWINSPAN groupings at 5 and 20 m in Lake Ontario. TWINSPAN was based on detailed taxonomic groups.

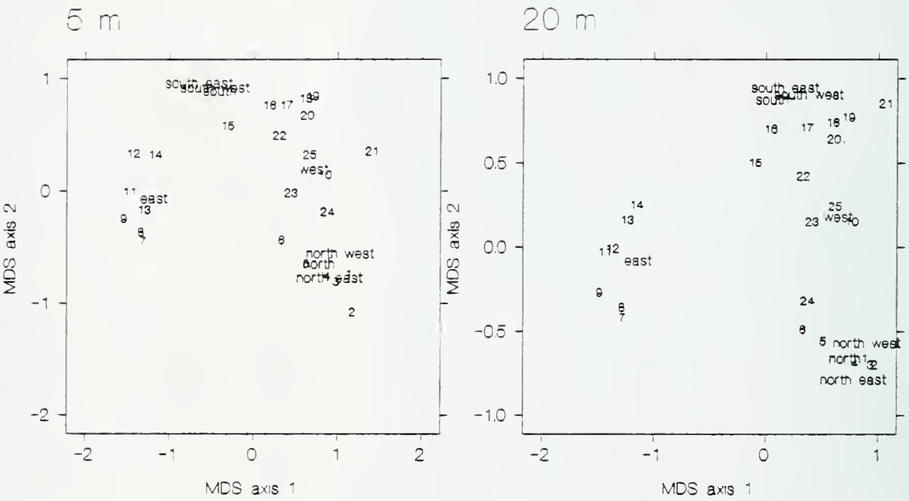

Figure 30. Scatter plot of ordination (MDS) axes 1 and 2 for Transects (a) and compass directions (b).

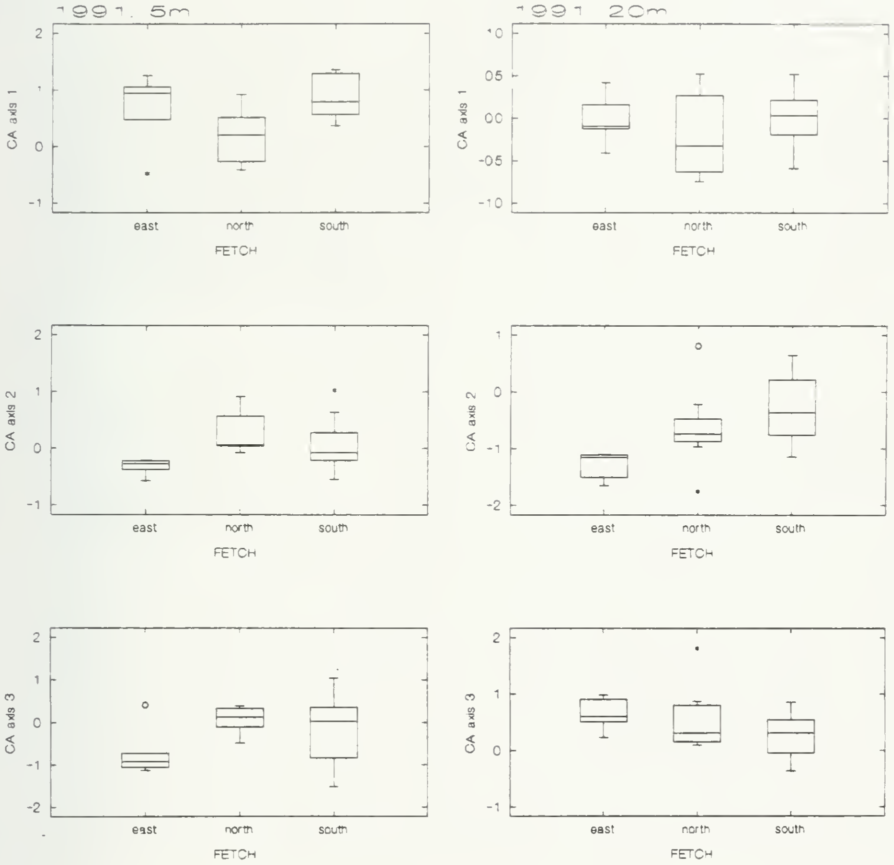

Figure 31. Box plots of CA axis scores in relation to the three exposure zones at 5m in 1981 and at 20 m in 1991.

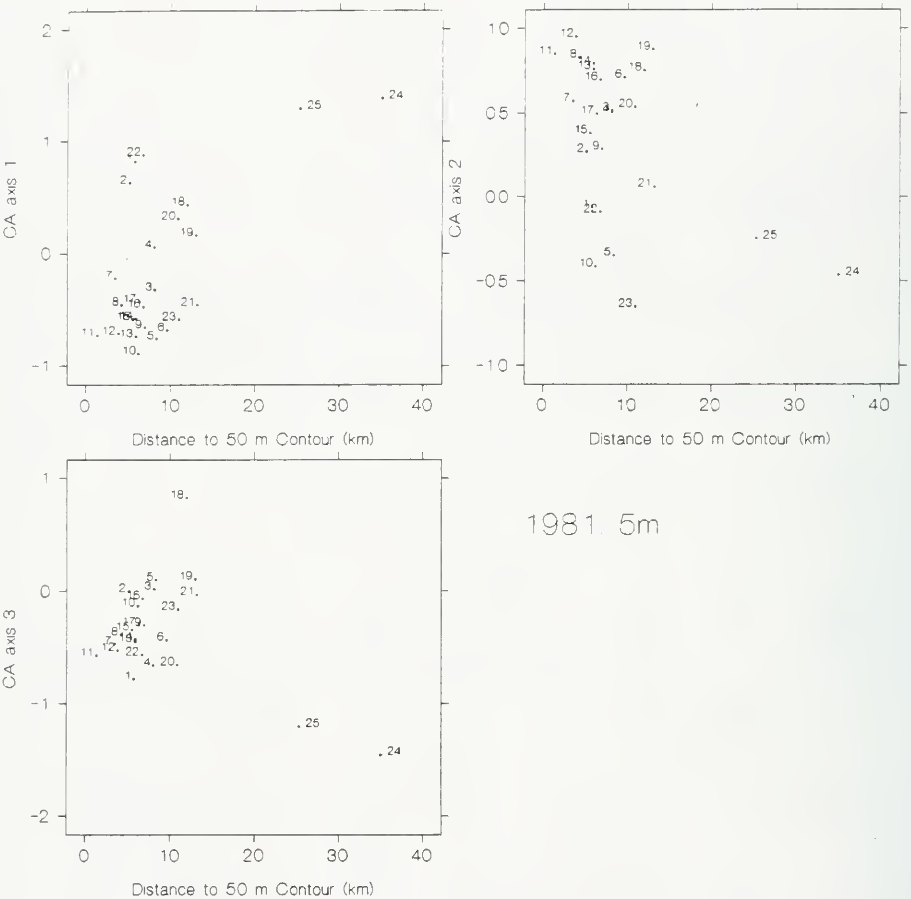

Figure 32. Scatter plot of CA axis scores showing the relationship between community structure and distance to the 50-m contour at 5 m in 1981.

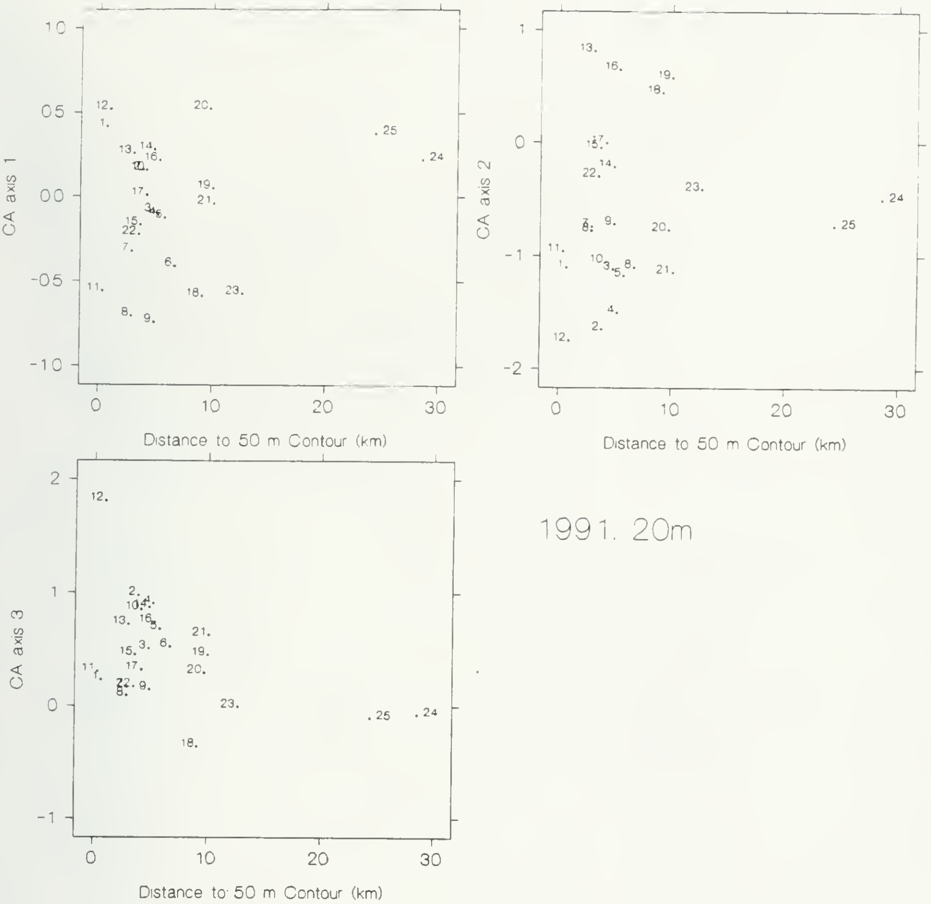

Figure 33. Scatter plot of CA axis scores showing the relationship between community structure and distance to the 50-m contour at 20 m in 1991.

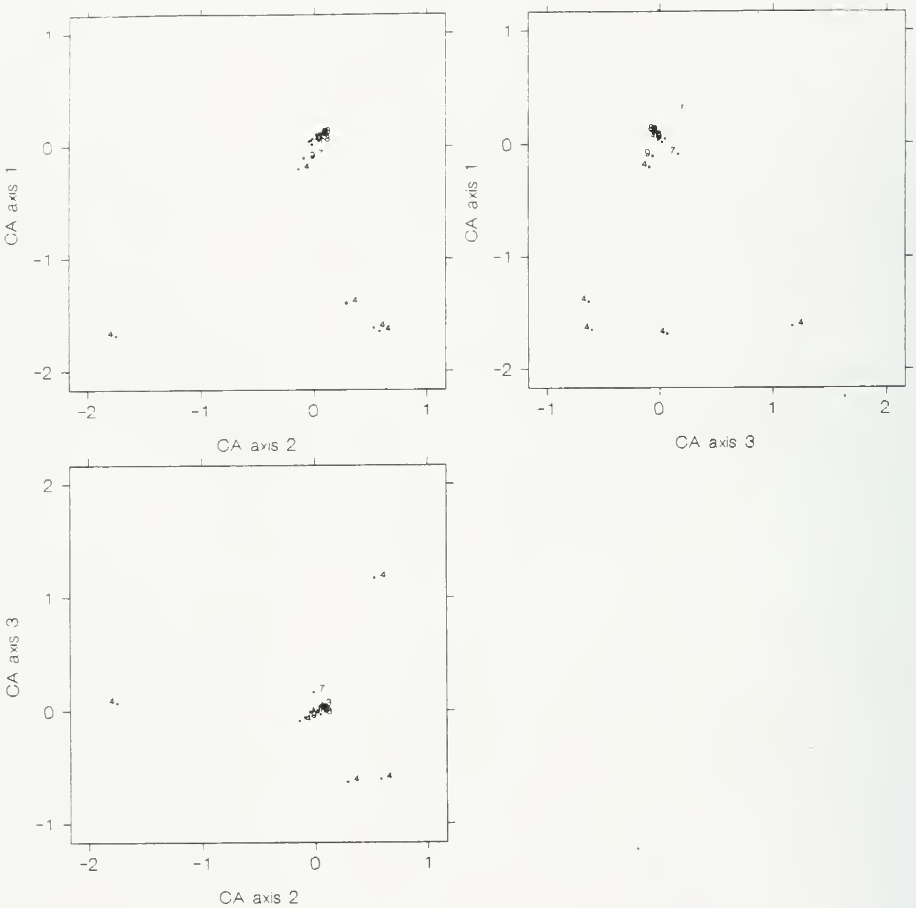

Figure 34. Scatterplot of Correspondence Analysis (CA) axis scores showing the associations among bivalve samples.

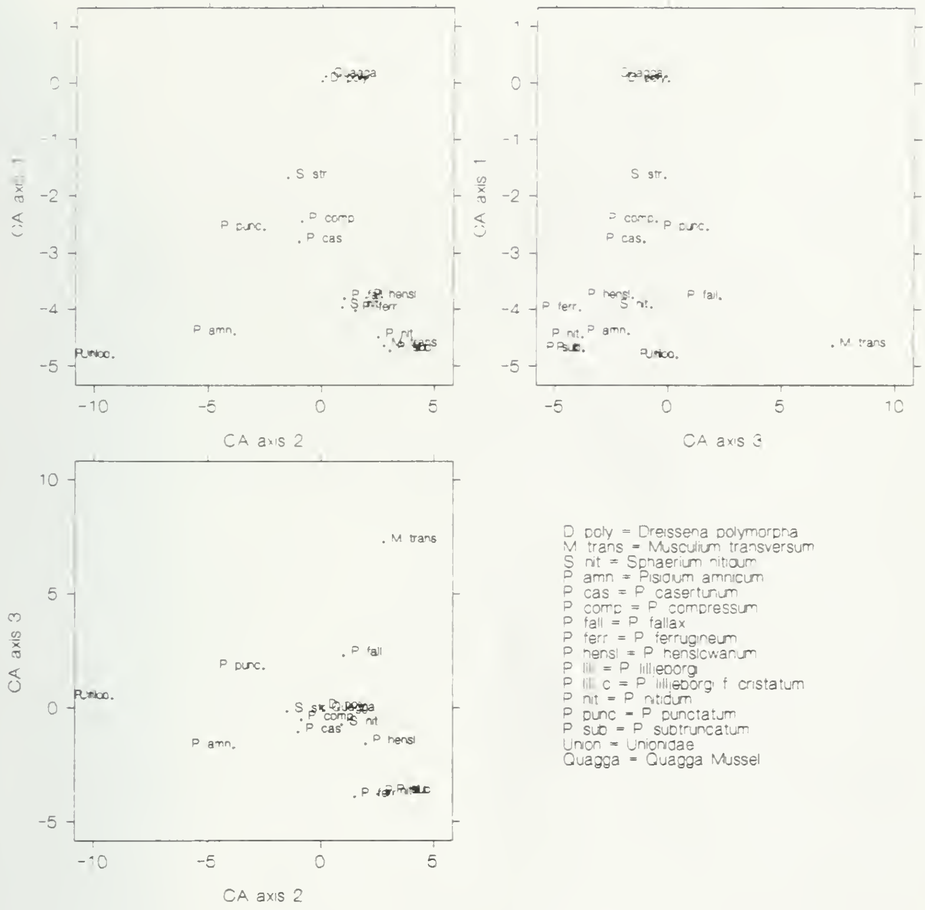

Figure 35. Scatterplot of Correspondence Analysis (CA) axis scores showing the associations among bivalve taxa. CA was based on 40 samples collected at 5 m at 8 transects between Niagara-On-The-Lake and Toronto.

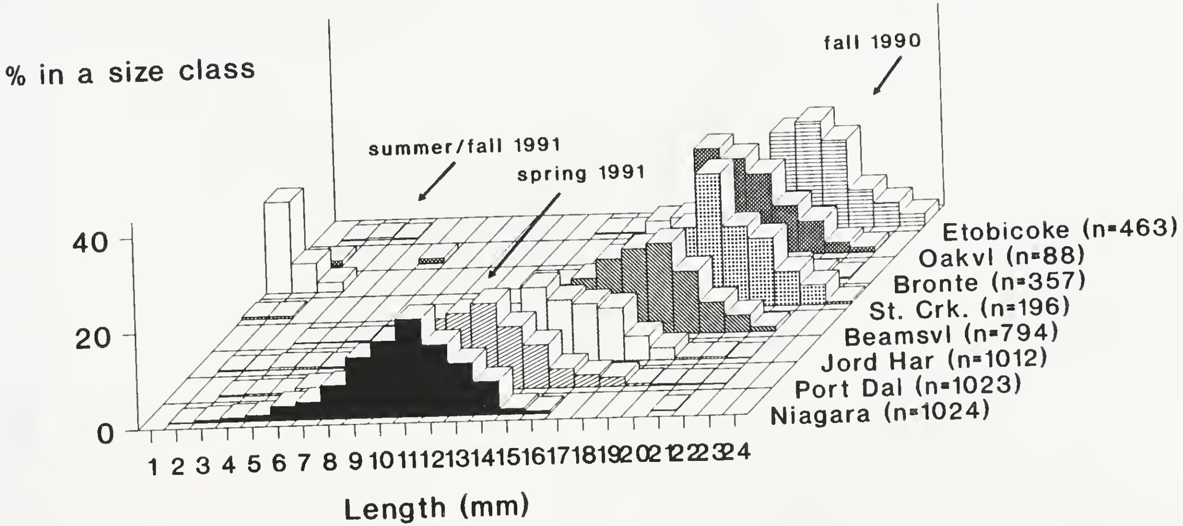

Figure 36. Variations in shell length of zebra mussels collected from transects between Niagara and Toronto in Lake Ontario.